The impact of herbivores on the natural regeneration of temperate deciduous woodland

Mallinson, Julian Robert

THE IMPACT OF HERBIVORES ON THE NATURAL REGENERATION OF TEMPERATE DECIDUOUS WOODLAND

Julian Robert Mallinson

Department of Biological Sciences
University of Durham

A thesis submitted for the degree of Doctor of Philosophy
University of Durham, 1999

To my family and friends

DECLARATION

I declare that this thesis is original and entirely my own work, except where otherwise stated. No part of it has been submitted previously for a degree at any other university.

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ABSTRACT

Many studies have reported deficient or intermittent patterns of natural regeneration in temperate deciduous woodland. The present study aimed to assess the relative impact of herbivore-mediated plant mortality on the natural regeneration dynamics of representative tree species (*Acer pseudoplatanus, Betula pendula, Fraxinus excelsior, Ilex aquifolium, Sorbus aucuparia, Taxus baccata and Ulmus glabra*) in representative temperate deciduous woodland (Shipley Wood and Derwent Gorge, County Durham). Sapling density and the density, spatial association and size distribution of adult tree populations varied significantly between tree species and study sites, reflecting contrasting patterns of current and historical regeneration.

Rates of post-dispersal seed predation and seedling herbivory were quantified using field-based 'cafeteria' trials. Rodents were the principal agents responsible for seed predation, whereas seedling herbivory was attributable to a mixed suite of herbivores including invertebrates, rodents and larger mammals. Rates of seed predation and seedling herbivory varied significantly between tree species, most likely reflecting individualistic, trade-off responses to chemical and physical attributes. Fine-scale spatial variation most likely reflected the preferential foraging of rodents beneath protective vegetation cover. There was no consistent evidence to support the hypothesis that dispersed seeds may escape disproportionately high offspring mortality beneath parent plants resulting from increased herbivore activity.

Natural seedling density varied significantly between years and between tree species, according to the abundance of viable seeds produced by conspecific adult trees. Although seedling survivorship varied significantly between species, the survivorship of each species was similar between years and between cohorts of the same year. Canopy cover, field layer cover or correlated factors were significant determinants of seed germination and seedling emergence, establishment and survival, according to age- and species-specific tolerances.

In relative terms, patterns of natural regeneration were primarily herbivore-limited (*Acer* and *Taxus*), microsite-limited (*Betula*, *Fraxinus*, *Ilex* and *Ulmus*) or limited by herbivores and microsites (*Sorbus*). The availability of viable seeds may have also limited the recruitment of *Ilex*, *Sorbus*, *Taxus* and *Ulmus*. Vegetative expansion, mast seeding, seed bank regeneration and repeated, prolonged reproduction may have reduced the actual impact of herbivory on natural regeneration, such that long-lived iteroparous tree species were unlikely to have been critically dependent on current recruitment.

ACKNOWLEDGEMENTS

I am particularly indebted to my supervisors, Phil Hulme and Brian Huntley, for their continued guidance, interest and support. I greatly appreciate the advice, time and encouragement they generously gave.

I would like to thank Eric Henderson, Michael Bone, Gordon Bainbridge, Margaret Turner and Paul Simpson for all their technical assistance. I am also grateful to Phil Gates, Dave Hyde, Mike Stacey and Peter Evans for their kind support.

I have had the privilege of working alongside fantastic lab-mates, including Dawn Scott, Steve Willis, Liam Simms, Yih-Yia Liao, Panos Giannakos, Laura Bonesi and Caroline Laburn. Thanks for answers to questions, stimulating discussion, coffee breaks, inspiration, stress relief, nights out and friendship. These are precious memories.

I am also grateful to fellow ecologists Mark O'Connell, Sean Twiss, Kate Lewthwaite, Larry Griffin and Claire McSorley for their advice and encouragement. Special thanks go to Justin Slowey for his great company and assistance in the field.

I would like to thank Lambton Estates, Mr. P. Oughtred and Mr. W. Metcalf for kindly permitting access to study sites and Simon Walker of English Nature for providing further support in the field.

Research was funded by a University of Durham Teaching Assistantship to Julian Mallinson.

This thesis is dedicated to my family and friends. Thanks for everything.

"The architect, by the relationships which he creates he wakes in us profound echoes, he gives us the measure of an order which we feel to be in accordance with that of our world, he determines the various movements of our heart and of our understanding. It is then that we experience the sense of beauty"

Le Corbusier

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CHAPTER 1

GENERAL INTRODUCTION

1.1 GLOBAL VEGETATION PATTERNS

It is well established that large-scale, geographic patterns of global vegetation are determined by climatic variables, particularly the seasonality of temperature and precipitation, that may be incorporated into classification schemes and predictive models to describe the physiognomy and distribution of plant formations, or 'biomes' (Holdridge, 1947; Guetter & Kutzbach, 1990; Prentice *et al.*, 1992).

Forest ecosystems account for more than fifty per cent of total biosphere net primary productivity and more than eighty-five per cent of total biosphere biomass (Ricklefs, 1990; Whittaker & Likens, 1975). In a global biome model, Prentice *et al.* (1992) distinguished seven dominant tree types and ten unique combinations of dominant tree types that were constrained by the primary driving variables of annual accumulated temperature over 5°C, mean coldest month temperature and an index of drought incorporating the available water capacity of soil and the seasonality of precipitation (Tables 1.1 and 1.2). Tropical rain forest, dominated by tropical evergreens, was predicted to occur only in the wettest regions of the tropics (precipitation >95% of evaporative demand), where the mean temperature of the coldest month was greater than 15.5°C. In contrast, boreal evergreen and summergreen dominated taiga was predicted to occur where winters were cold (-19 to –35°C) and precipitation met over 75% of demand. Temperate summergreen trees, cool-temperate conifers and boreal summergreen trees dominated in temperate deciduous forest, that was predicted for climates with cool winters (-2 to 5°C) and 65% of precipitation demand , and those with colder winters (down to -15°C) where precipitation was insufficient (<75% of demand) for boreal evergreen conifers.

At a local scale, the unique interactions of climate, vegetation, topography and parent materials determine the characteristics of soils and the biological systems they support (Archibold, 1995). Intraspecific and interspecific competition for resources within plant communities and the loss of photosynthetic and reproductive material to herbivores may also influence plant recruitment and community composition.

Table 1.1. Dominant tree types and corresponding environmental constraints (T_c, mean temperature of coldest month; GDD_{min}, growing degree-days over 5°C; α, Priestley-Taylor coefficient of annual moisture availability) described by Prentice *et al.* (1992).

Tree type	T_c		GDD_{min}	α	
	Min	max		min	Max
Tropical evergreen	15.5			0.80	
Tropical raingreen	15.5			0.45	0.95
Warm-temperate evergreen	5			0.65	
Temperate summergreen	-15	15.5	1200	0.65	
Cool-temperate conifer	-19	5	900	0.65	
Boreal evergreen conifer	-35	-2	350	0.75	
Boreal summergreen		5	350	0.65	

Table 1.2. Combinations of dominant tree types constituting forest biomes described by Prentice *et al.* (1992).

Forest biome	Dominant tree types
Tropical rain forest	Tropical evergreen
Tropical seasonal forest	Tropical evergreen, Tropical raingreen
Tropical dry forest/savanna	Tropical raingreen
Broad-leaved evergreen/ warm mixed forest	Warm-temperate evergreen
Temperate deciduous forest	Temperate summergreen, Cool-temperate conifer, Boreal summergreen
Cool mixed forest	Temperate summergreen, Cool-temperate conifer, Boreal evergreen conifer, Boreal summergreen
Cool conifer forest	Cool-temperate conifer, Boreal evergreen conifer, Boreal summergreen
Taiga	Boreal evergreen conifer, Boreal summergreen
Cold mixed forest	Cool-temperate conifer, Boreal summergreen
Cold deciduous forest	Boreal summergreen

1.1.1. **Characteristics of temperate deciduous forest**

Climatic conditions in temperate forest regions alternate between warm, moist summers and mild winters. Seasonality is determined more by temperature than by precipitation, according to latitude and continentality. Seasonal variation has favoured

the widespread development of deciduous broad-leaf forests in the northern hemisphere (western and central Europe, eastern Asia and eastern North America) (Archibold, 1995). In the southern hemisphere, temperate deciduous forests are restricted to the drier parts of the southern Andes. Deciduous tree species are replaced by conifers on higher slopes and broad-leaved evergreens in more southerly locations (Eyre, 1968), reflecting gradients of temperature and drought, respectively.

Although most of lowland Europe receives between 500 and 750mm annual precipitation, climatic conditions become progressively drier eastwards towards the continental interior (Archibold, 1995). In maritime locations, including the British Isles, temperatures typically average 3-5°C in the winter and 15-17°C in the summer, rarely exceeding 30°C. In contrast, average summer temperature increases to approximately 22°C eastwards through the temperate deciduous forest region of central Russia and average winter temperatures decrease from -4 to -15°C.

The vegetation dynamics of temperate deciduous forest reflect the physiological responses of plants to seasonal variation in climate (Archibold, 1995). Tree growth resumes in the spring in response to longer day lengths and increasing temperatures. Incident radiation penetrating to the forest floor decreases from 50-70% when trees are leafless, to less than 10% when leaves are fully expanded (Tasker & Smith, 1977). Consequently, many shade-intolerant herbaceous species flower in the early spring to precede the maximum cover of the canopy. These are replaced by more shade-tolerant species as the canopy develops and by evergreen species in autumn and winter. Tree species also vary in light requirements, reflecting competitive ability and successional status. Leaf senescence marks the end of the growing period, when trees enter leafless winter dormancy in response to shorter days and cooler temperatures. Deep innate dormancy is typically broken by exposure to low temperatures for more than one month, until chilling requirements have been satisfied. Long, warm spring days then stimulate bud break and the growth of new buds and twigs.

In mature temperate deciduous forest, net primary productivity averages 10 tonnes per hectare per year and plant biomass typically ranges from 120 to 300 tonnes per hectare above ground and 30 to 80 tonnes per hectare as roots (DeAngelis *et al.*, 1981, cited in Archibold, 1995). In European mixed oak forest, Duvigneaud & Denaeyer-De Smet (1970) estimated the partitioning of total aerial production each

year between new woody growth (50%), new foliage (26%) and fruits, flowers and other materials returned as litter (17%). Shrub and herbaceous field layer species contributed a further two and five per cent of total annual production, respectively. Excluding large trunks, litterfall in deciduous forest ranges from 324 to 624 grams per square metre per year, with leaves contributing 53 to 88 per cent of total litterfall (DeAngelis *et al.*, 1981, cited in Archibold, 1995).

Soils of the European deciduous forest region are characterised by abundant biological activity, high nutrient content and a deep, rich humus layer. These 'brown earths' are slightly acidic, typically ranging from pH 5.5-6.5. 'Podsols' may develop beneath dense deciduous woodland where cool humid conditions, canopy shade or an accumulation of acid litter slow decomposition (Mackney, 1961).

Regeneration within established temperate woodland is largely confined to openings in the canopy, or 'gaps', created by disturbances (Peterken, 1996). Accordingly, gap-phase regeneration is spatially and temporally irregular; its timing and composition depending on gap size, the coincidence of mast seeding and gap formation, and the response of individual species to the dynamics of canopy structure and ground conditions. Small canopy gaps, formed by the loss of individual trees or small groups, are more typical of temperate woodland than large canopy gaps, created by catastrophic disturbances. In Britain, wind is the principal source of canopy disturbance, although fire, drought, pathogenic fungi, herbivory, flood damage, snow and ice may occasionally cause substantial damage to natural woodland.

Five unique responses to gap-formation have been recognised (Bazzaz, 1983, cited in Peterken, 1996); 1) *Crown expansion* - canopy gaps closed by lateral growth of canopy, subcanopy and understorey trees and shrubs; 2) *Sprouting from mature trees* - sprouts arising from snags, prostrate trunks and layered branches, often of individuals damaged in disturbance event; 3) *Advance regeneration* - anticipatory regeneration of shade-tolerant species from seedlings and saplings established beneath undisturbed canopy; 4) *Seedling regeneration* - regeneration of seedlings established after disturbance from dormant or recently dispersed seeds derived from a local source; 5) *Regeneration from immigrant seed* - regeneration of seedlings established after disturbance from seeds derived from a distant source. The significance of each regeneration response depends on the species involved and the scale, severity and

duration of the disturbance event. Seedling regeneration and vegetative regrowth most likely constitute a mixed response to mild, small-scale disturbances of short duration.

1.1.2. **Status of temperate deciduous forest**

Although temperate deciduous trees are widely distributed throughout Europe, much of the continuous forest cover has been historically removed for agriculture, and that which remains is predominantly secondary growth that has recolonised abandoned farmland and logged sites (Archibold, 1995). Invariably, these semi-natural woodlands are fragmented in their distribution, representing 'island' communities within an agricultural and urban landscape, and are subject to varying degrees of human disturbance.

A fragmented woodland system may be far from stable, since there is a minimum critical island size necessary to perpetuate natural forest conditions and the survival of native plant and animal species. Forest edges have higher tree density and species richness than forest interiors, and are dominated by shade-intolerant species that are dependent on side lighting and the drying effects of wind (Ranney *et al.*, 1981). Since the proportion of edge per unit area of forest increases progressively with decreasing island size, forest fragmentation would favour edge species (shade-intolerant) over interior species (shade tolerant), depending on the frequency and size of existing canopy gaps (Levenson, 1981).

Changes in forest structure and distribution following clearance may also influence the composition of fauna. Although many species have been able to adapt to the changed conditions, becoming more widely distributed, others have disappeared from forest island communities. Whitcomb *et al.* (1981, cited in Archibold, 1995) found that forest island size was negatively correlated with bird density and positively correlated with the diversity of species associated with the forest interior, according to species-dependent minimal area requirements. The number of 'edge' species also increased in smaller forest islands (consistent with Hoffmeyer & Hansson (1974) for *Apodemus* spp.), whereas generalist species that occupied a variety of habitats occurred at a similar frequency in all sizes of forest island.

1.2. REGULATION OF PLANT POPULATIONS AND COMMUNITIES

An understanding of the principal factors underlying plant demography and community structure is clearly fundamental to the conservation of existing temperate

deciduous woodland. Many interacting biotic and abiotic factors have been found to influence plant survival and reproduction, according to physiological, morphological and phenological plant traits (Crawley, 1997). Environmental determinants of plant performance include fire, drought, waterlogging, shade, disturbance, low nutrient availability, soil acidity, heavy metals, atmospheric pollutants, wind exposure and extremes of temperature. For example, large seeds of *Castanea mollissima* and *Quercus rubra* produce vigorous seedlings beneath dense shade, whereas small-seeded light-demanding species, including *Betula lenta* and *B. populifolia*, grow poorly beneath shade (Grime & Jeffrey, 1965). Ring porous woods, including *Quercus* spp., are particularly sensitive to xylem breakage during freeze-thaw cycles, while diffuse porous woods, including *Betula* spp., are able to maintain hydraulic conductance (Sperry *et al.*, 1994). Drought desiccation (Watt, 1919) and low temperature (Jones, 1959) may also limit the germination of *Quercus* spp. seeds. Many deciduous trees, including *Betula* spp. and *Populus* spp., regenerate after fire by sprouting from surviving stems or root stocks (Crawley, 1997) and certain wind-dispersed species, including *Acer* spp. or *Fraxinus* spp., are able to persist in habitats subject to erratic, large-scale disturbance (Grime, 1979). In oak woodland, Goldberg (1985) found that *Lysiloma divaricata* only survived on acid soil if soil pH was artificially increased, whereas *Quercus albocincta* showed no significant response to increased soil pH.

Biotic interactions influencing plant demography and community structure include disease, parasitism, intra-specific competition and inter-specific competition. For example, competition with herbs may significantly reduce the growth of tree and shrub seedlings, including *Acer rubrum* (red maple) and *Cornus racemosa* (gray dogwood) (Gill & Marks, 1991). In deciduous forest, Goldberg (1985) found that the removal of field-layer vegetation was necessary to prevent the competitive exclusion of *L. divaricata* and *Q. albocincta* seedlings. Streng *et al.* (1989) reported that damping-off disease and proximity to conspecific adults were significant factors limiting the recruitment of tree species, including *Acer rubrum* and *Ulmus americanum* (american elm). Many investigations have also found 'herbivory', the consumption of living plant material by animals, to be a critical factor influencing plant performance and demography (Crawley, 1988).

1.3. IMPACT OF HERBIVORES ON PLANT PERFORMANCE

The diversity of herbivores is reflected in the diversity of feeding habits and plant tissues consumed (Table 1.3). Relative to decomposers, herbivores consume a relatively low proportion of net primary productivity, averaging ten per cent in most natural ecosystems (Crawley, 1983). It is the timing, specificity and intensity of herbivory that determine the impact of herbivores on plant performance. For example, nectar drinking, bud removal and wood felling (Table 1.3) are likely to have markedly different influences on plant survival and reproduction.

Herbivores may have either direct or indirect effects on plant communities. Indirect effects include defoliation that influences habitat structure and the microclimate (including temperature, relative light intensity and airflow) experienced by other plant species. Herbivory may also influence nutrient cycling, through the input of readily available nutrients, including faeces and carrion (Duffey *et al.*, 1974; Owen, 1980), the outflow of nutrients following severe defoliation (Swank *et al.*, 1981) or the increase of light penetration, soil temperature and organic decomposition (Collins, 1961). Large herbivores may also alter soil structure by compaction and puddling, influencing plant community composition (Duffey *et al.*, 1974).

1.3.1. **Impact on plant survival**

Under certain circumstances, rates of herbivory may be sufficient to directly influence plant survival. For example, at a peak density of over one hundred per hectare, populations of *Lepus americanus* (snowshoe hare) stripped and decapitated more than one million young *Pinus banksiana* (jack pine), leaving only forty undamaged trees within an area of ten hectares (Rowan, 1954). Populations of *Loxodonta africana* (African elephant) may also destroy vast numbers of trees when elevated above local carrying capacity (Kortland, 1984), such as in *Terminalia glaucescens* woodland when herbivore-mediated tree mortality increased from twenty-four to ninety-six per cent over a nine year period (Laws *et al.*, 1975). Peterken (1966) also recorded severe herbivore-mediated tree mortality following winter browsing by rodents and deer. After five years, the survival of *Ilex aquifolium* (holly) was only 7.3% under open pines and 0.008% under deep conspecific shade. Edenius (1993) simulated the winter browsing of *Pinus sylvestris* (scots pine) by *Alces alces* (moose) and found that tree mortality often occurred two or more years

Table 1.3. Plant tissues and the herbivores that feed on them (Reproduced from Crawley, 1983).

Tissue	Mode of feeding	Examples of feeders
Leaves	Clipping	Ungulates, slugs, sawflies, butterflies, etc.
	Skeletonizing	Beetles, sawflies, capsid bugs
	Holing	Moths, weevils, pigeons, slugs, etc.
	Rolling	Microlepidoptera, aphids
	Spinning	Lepidoptera, sawflies
	Mining	Microlepidoptera, Diptera
	Rasping	Slugs, snails
	Sucking	Aphids, psyllids, hoppers, whitefly, mites, etc.
Buds	Removal	Finches, browsing ungulates
	Boring	Hymenoptera, Lepidoptera, Diptera
	Deforming	Aphids, moths
Herbaceous stems	Removal	Ungulates, sawflies, etc.
	Boring	Weevils, flies, moths
	Sucking	Aphids, scales, cochineals, bugs
Bark	Tunnelling	Beetles, wasps
	Stripping	Squirrels, deer, goats, voles
	Sucking	Scales, bark lice
Wood	Felling	Beavers, large ungulates
	Tunnelling	Beetles, wasps
	Chewing	Termites
Flowers	Nectar drinking	Bats, humming-birds, butterflies, etc.
	Pollen eating	Bees, butterflies, mice
	Receptacle eating	Diptera, microlepidoptera, thrips
	Spinning	Microlepidoptera
Fruits	Beneficial	Monkey, thrushes, ungulates, elephants
	Destructive	Wasps, moths, rodents, finches, flies, etc.
Seeds	Predation	Deer, squirrels, mice, finches, pigeons
	Boring	Weevils, moths, bruchids
	Sucking	Lygaeid bugs
Sap	Phloem	Aphids, whitefly, hoppers
	Xylem	Spittlebugs, cicadas
	Cell contents	Bugs, hoppers, mites, tardigrades, etc.
Roots	Clipping	Beetles, flies, rodents, ungulates, etc.
	Tunnelling	Nematodes, flies
	Sucking	Aphids, cicadas, nematodes, etc.
Galls	Leaves	Hymenoptera, Diptera, aphids, mites
	Fruits	Hymenoptera
	Stems	Hymenoptera, Diptera
	Roots	Aphids, weevils, Hymenoptera

after severe browsing.

Although mature perennial plants with submerged perennating organs adequately survive a single defoliation, repeated successive defoliations may deplete resources sufficiently to reduce survival rates. For example, defoliation by *Malacosoma disstria* (forest tent caterpillar) did not significantly influence the mortality of *Populus tremuloides* (quaking aspen) unless trees were subject to three successive heavy defoliations (Churchill *et al.*, 1964). Similarly, Stephens (1971, cited in Crawley, 1983) found that three successive heavy defoliations of *Quercus* sp. by *Lymantria dispar* (gypsy moth) resulted in mortality rates of up to eighty per cent, compared to only five per cent mortality following a single defoliation, consistent with natural rates of survival. However, mortality rates were significantly greater following single defoliations of *Pinus strobus* (white pine, 28%) and *Tsuga canadensis* (hemlock, 68%).

In many cases, the impact of herbivory is disproportionately greater than the extent of tissue removal. For example, ring-barking and bark-stripping by vertebrate herbivores, including Rodentia, Lagomorpha and Artiodactyla, has the effect of separating phloem and cambial tissue from woody xylem and breaking the carbohydrate link between leaves and roots, often resulting in tree mortality (Gill, 1992). Similarly, slugs may severely damage newly established plant populations by felling young shoots at ground level (Harper, 1977). Plants are effectively destroyed despite the consumption of relatively little tissue.

Disproportionate mortality may also follow herbivory by insects that directly attack phloem and cambial layers or indirectly act as vectors for plant pathogens. Species of elm bark beetle (*Scolytus* spp. and *Hylurgopinus rufipes*), for example, are responsible for the transmission of the Dutch elm disease fungus, *Ceratostomella ulmi*, which causes mortality by blocking phloem (Strobel & Lanier, 1981). Dixon (1971) found that the removal of phloem sap from saplings of *Tilia vulgaris* (common lime) by *Eucallipterus tiliae* (lime aphid) had the effect of suppressing root growth, which subsequently restricted total mass increase to eight per cent that of uninfested saplings.

1.3.2. **Impact on plant growth**

Herbivores may directly reduce plant growth by reducing photosynthetic area and rates of assimilation (leaf damage), interfering with water uptake, nutrient uptake and carbohydrate flow (stem and root damage) and weakening the physical structure of the plant (stem damage) (Crawley, 1983). Increased susceptibility to pathogens and the diversion of production to wound repair are also likely to suppress plant growth and reproduction. In *Pinus-Sorbus* forest, Dinesman (1967) recorded a reduction of forage biomass from 181 to 109 kg ha^{-1} following browsing by *Alces alces*. Of this biomass reduction, only 3.5 kg ha^{-1} resulted directly from consumption, with the remaining 68.5 kg ha^{-1} resulting from the reduced growth of damaged trees. McInnes *et al.* (1992) also found that browsing by *A. alces* significantly decreased tree biomass (from 230 to 150 trees ha^{-1}), preventing the recruitment of preferred saplings and reducing canopy tree diversity. Bergstrom & Danell (1995) artificially stripped the long-shoot leaves of *Betula pendula* to simulate browsing by *A. alces* and recorded reduced shoot height growth and leaf biomass in the year following damage. Xylem-feeding by *Magicicada septendecim* (cicada) was effective in reducing ring width in the wood of *Quercus ilicifolia* (scrub oak) by up to thirty per cent, without influencing fecundity (Karban, 1980).

The timing of defoliation is critical when leaves are produced synchronously. For example, when adults of *Quercus* spp. were defoliated by seventy-five per cent early in the growing season, wood production was reduced by fifty per cent, whereas subsequent removal at a similar intensity had a negligible effect on growth (Franklin, 1970; Rafes, 1970). Plants are particularly tolerant of grazing when the continuous production of new leaves is able to compensate for the loss of young leaves.

Herbivores may also influence plant shape by browsing leading shoots and terminal leaf buds, promoting lateral growth and branching, or browsing lower foliage leaving high inaccessible crowns (Crawley, 1997). Galling insects may also generate distinctive plant morphologies. Plant size distribution may depend on herbivore preferences, according to plant susceptibility (Crawley, 1983).

1.3.3. **Impact on plant fecundity**

Reduced photosynthetic area and carbohydrate assimilation following significant defoliation may also reduce plant fecundity. For example, when Rockwood (1973) subjected six Costa Rican tree species to two artificial defoliations in the same

year, eighty per cent of the defoliated trees failed to fruit, while only thirty per cent of the intact trees lacked fruit. Stickler & Pauli (1961) found that the removal of young upper leaves, as often occurred during browsing, was much more significant in reducing fecundity than removing older leaves. As seed production is typically carbohydrate-limited, defoliation is most likely to influence fecundity when plants are competing for resources, including light (Crawley, 1983). Root-feeding herbivores that reduce water uptake, nutrient uptake and carbohydrate flow may also reduce plant fecundity and lead to increased herbivory by leaf-feeding insects (Crawley, 1997).

Herbivores reduce plant fecundity directly by destroying flowers on the plant. In forests of *Pinus radiata* (Monterey pine) in New Zealand, for example, *Trichosurus vulpecula* (common bushtail possum) consume large quantities of pollen prior to anthesis and female strobili between pollination and fertilisation, which may combine to reduce seed production by up to forty per cent (Crawley, 1983). At the same time, *Fringilla coelebs* (chaffinch) may also destroy up to fifty per cent of developing female strobili. In southern England, the gall wasp *Andricus quercus-calicis* infests acorns of *Quercus robur* (pedunculate oak), which responds by shedding the entire peduncle (Darlington, 1974). The total loss of infested and uninfested acorns may exceed ninety per cent.

Herbivory may delay plant flowering, as a result of either flower bud damage or a reduction in protein and carbohydrate supply (Crawley, 1983). This may be particularly detrimental to plant fecundity if exposure to frost damage is increased late in the season or rates of encounter with pollinators are reduced. In general, the impact of herbivory on plant fecundity depends on the timing of defoliation and the potential for compensation. Early defoliation following synchronous leaf production may reduce or completely inhibit flowering, whereas defoliation may have little effect on the fecundity of plants with continuous leaf production (Crawley, 1983). Seed production is particularly sensitive to herbivory, with a reduction in seed size or seed production typically following defoliation subsequent to flowering. Fruiting trees of *Quercus robur* from which all herbivorous insects had been removed consistently produced 2.5 to 4.5 times more seeds than fruiting trees from which insect herbivores had removed 8-12% leaf area (Crawley, 1985).

1.3.4. **Anti-herbivore defence**

Herbivores may influence plant growth and fecundity indirectly, when plants are required to redirect production toward wound repair, defensive structures and inducible toxins that afford some degree of protection against herbivore attack.

In many plants, defence mechanisms are induced as a direct response to herbivory. *Pinus sylvestris*, for example, modifies phenol metabolism to produce novel defensive chemicals following damage by *Neodiprion sertifer* (european pine sawfly) (Thiegles, 1968). Defensive compounds are produced secondary to principal biochemical processes and include enzyme inhibitors, haemagglutinins and cyanogenic glucosides (Freeland & Janzen, 1974).

'Rapidly-inducible' chemical defences, typically protease inhibitors, may significantly reduce subsequent herbivore damage. For example, Bryant & Kuropat (1980) found that leaves of *Betula papyrifera* ssp. *humilis* (Alaska paper birch) that had regenerated after severe defoliation were significantly more resistant to attack from *Lepus americanus* (snowshoe hare). Similarly, the defoliation of *Larix decidua* (European larch) by *Zeiraphera diniana* (larch budmoth) resulted in delayed leaf production, lower nitrogen levels, higher fibre and resin concentration, and tougher leaves, which in turn suppressed the survival and adult fecundity of moths over the subsequent four to five years (Baltensweiler *et al.*, 1977). Fowler & Lawton (1985), however, found only limited evidence to support the effectiveness of rapidly-inducible plant defences against insect herbivores. West (1985) provided unequivocal evidence that plant defensive responses may directly influence the dynamics of a herbivore population. When twenty-five per cent leaf area was artificially removed from adult *Quercus robur*, deaths of lepidopterous leaf-mining larvae (*Phyllonorycter* spp.) from unknown causes were fifty to one hundred per cent greater than controls.

Plants may be distinguished according to the probability that they will be encountered by animal grazers (Feeny, 1976). Species that are 'apparent' to herbivores tend to occur conspicuously in specific habitats, depending on non-selective, dose-dependent defence mechanisms to reduce grazing intensity. The distribution of 'unapparent' species tends to be patchy and unpredictable, incorporating a number of habitat types and secondary defences, which provide further protection from specific herbivores.

1.3.5. **Plant compensation**

Plants exhibit a variety of mechanisms that may partially or fully compensate for the effects of herbivory. Plant compensation was reported by Nielsen & Ejlerson (1977) investigating the defoliation of *Fagus sylvatica* (beech) by the weevil *Phyllobius argentatus*. The consumption of lower shaded leaves, with low rates of photosynthesis and normal rates of respiration, had little effect on tree productivity by improving the overall balance between photosynthesis and respiration. Alternatively, the removal of upper leaves from a plant may increase light penetration and the rate of photosynthesis of previously shaded lower leaves.

Many plants compensate for herbivory by the mobilisation of stored carbohydrates. Kigel (1980) found that plants with greater carbohydrate reserves had higher initial rates of leaf regrowth following complete defoliation. Seedling-like plants of *Quercus robur* continued to regenerate one-year-old shoots after as much as twenty years of repeated browsing to ground level by rabbits (*Oryctolagus cuniculus*) (Crawley & Long, 1995).

Plants may also shift the distribution of photosynthate following herbivory in order to maintain a balanced shoot/root ratio. Typically, when roots are damaged, an increased proportion of net production is directed towards root growth, and when shoots are defoliated, the shift is towards shoot growth (Crawley, 1983). Alternatively, plant defoliation may increase the photosynthetic rate per unit area of surviving leaf ('unit leaf rate', ULR), stimulate the development of buds that would otherwise remain dormant or increase the subsequent survival of remaining plant parts. When leading shoots of *Pinus sylvestris* were artificially defoliated to simulate herbivory, the growth of new shoots below the damage was increased (Honkanen *et al.*, 1994). Damage to buds also had a positive effect on growth. Plant competition may significantly influence the compensation response of herbivore-damaged plants. *Betula pendula* showed reduced growth following defoliation, irrespective of intraspecific competition, whereas browsed plants showed enhanced growth only when intra-specific competition was low (Hjalten *et al.*, 1993).

Alternatively, compensation may operate at a population level, when herbivore-mediated plant mortality has the effect of ameliorating intraspecific competition (Crawley, 1983). Reduced plant density and competition are compensated for by an increase in the net recruitment or net productivity of surviving plants.

Overall, moderate herbivory may replace natural rates of self-thinning, having little effect on equilibrium plant population density.

1.3.6. **Plant benefits from herbivore activity**

Although herbivores generally have a destructive influence on plant growth, fecundity and survival, there are many cases where plants benefit from the activity of herbivores. Such interactions, including the inadvertent transfer of pollen between flowering plants by animals consuming pollen and nectar, are more appropriately described as 'mutualistic'.

For many plant species, animals are necessary agents of primary and/or secondary seed dispersal (Murray, 1986; Chambers & MacMahon, 1994). Mechanisms of animal-dispersal include 'endozoochory', via the consumption and subsequent regurgitation or egestion of seeds, 'ectozoochory', the transport of seeds attached externally to animals and 'synzoochory', from the failed predation of cached seeds.

Seeds dispersed by ectozoochory become attached to the dispersal agent by either chemical (viscid exudates or mucilage) or physical (hooks or spines) adhesion. Whereas ectozoochory relies on the characteristics of diaspores, synzoochory is a function of the general behaviour of hoarding granivores. Caching is a means of hoarding food against subsequent periods of deprivation and concealing resources from intraspecific and interspecific competitors (Price & Jenkins, 1986). Seed germination and seedling establishment may follow if the cache remains undisturbed.

Dispersal by endozoochory (including Aquifoliaceae, Cornaceae and Rosaceae) may be deliberate or accidental, if animals feeding on foliage consume seeds not specifically adapted for dispersal. Alternatively, plants may invest in rewards, typically in the form of a fleshy fruit, to attract seed consumption. To prevent premature consumption, unripe fruit often contain toxic secondary compounds that are subsequently broken down during ripening. This is usually advertised by a colour change to which specialist frugivores, with colour vision, are likely to be sensitive. In temperate woodlands, birds are particularly important dispersers of seed by endozoochory (Snow & Snow, 1988) while carnivore species, including *Meles meles* (badger), *Martes foina* (stone marten), *Vulpes vulpes* (red fox) and *Ursus arctos* (brown bear) may be seasonally important (Herrera, 1989; Giannakos, 1997).

The dispersal of nut fruits by synzoochory (including Corylaceae, Fagaceae and Hippocastanaceae) is particularly effective in temperate regions where a seasonally severe climate favours the widespread hibernation of mammals and the accumulation of nut caches as winter food stores. However, seed production must be sufficient to compensate for the loss of dispersed seed to herbivores and unfavourable microhabitats. As a result of seed caching by *Eutamias amoenus* (Klamath chipmunk), *E. townsendii* (Townsend's chipmunk) and *Citellus lateralis* (golden-mantled ground squirrel), up to ninety per cent of *Purshia tridentata* (bitterbrush) seedlings emerged in clusters, consisting an average of twelve seedlings (West, 1968).

Herbivores were deterred by the infestation of *Crataegus monogyna* (hawthorn) fruits by insects (Courtney & Manzur, 1985) and *Apodemus sylvaticus* (woodmice) rejected acorns of *Quercus robur* that contained larvae of the weevil *Curculio glandium* (Crawley & Long, 1995). Since invertebrates are less likely to contribute to seed dispersal than vertebrates and partial damage may reduce seed palatability to vertebrates, the impact of invertebrates on plant processes is more likely destructive than beneficial. Although animal dispersal predominates in temperate deciduous woodland, the seeds of many trees (including Aceraceae, Betulaceae, Oleaceae and Ulmaceae) are dispersed by wind and invariably germinate in the spring following a period of dormancy (Grime *et al.*, 1988).

1.4. IMPACT OF HERBIVORES ON PLANT DEMOGRAPHY

The impact of herbivory on plant performance does not necessarily imply that herbivores significantly influence plant population dynamics. In fact, the precise mechanisms that regulate natural plant populations are poorly understood. In extreme cases, herbivory may directly cause the mortality of mature, established plants. More typically, however, mature plants compensate or defend against herbivore attack such that herbivory may only influence plant growth and fecundity or increase the susceptibility of mature plants to alternative mortality factors, such as water-logging, drought and air pollution (Crawley, 1988). Herbivores most often increase plant susceptibility to inter- and intra-specific competition (Whittaker, 1979, Crawley, 1988). Herbivory that has a negligible impact on plant mortality rate may be more appropriately considered as 'parasitism'.

Seedlings are particularly vulnerable to defoliation or suppression during early establishment when seed reserves have been depleted, growth and survival first depend on the products of photosynthesis and compensatory ability is least developed (Crawley, 1983). The destruction of seeds by herbivores is likely to have an even more predictably adverse effect on individual plants, when compensation is limited and a single attack may be sufficient to destroy the plant. Seeds and seedlings are also highly preferred by many herbivore species. The nutritional value of vegetation differs according to the content of lignin and other indigestible materials. Herbivores may assimilate only 15% of the energy in wood, relative to 30-40% in shrubby material, 60-70% in young vegetation and as much as 80% in seeds (Archibold, 1995).

Despite the extensive literature detailing the impact of herbivores on plant performance, relatively few studies have attempted to describe the complex interactions between herbivory and plant population dynamics (Crawley, 1988; Hulme, 1996b). Dramatic changes in plant communities following herbivore exclusion (Ross *et al.*, 1970; Linhart & Whelan, 1980) are more likely to support the regulation of plant populations by herbivory than the influence of herbivores on plant performance. Since herbivores principally influence the mortality of individual plants at seed and seedling stages, it is by the destruction of seeds and seedlings during plant recruitment that herbivores are most likely to regulate plant population dynamics via mortality.

1.4.1. **Impact on natural regeneration**

Evans (1988) broadly defines natural regeneration as "raising high forest from seed directly from parent trees...without resorting to planting, direct sowing or coppicing". Recruitment from seed follows a continuous multi-step sequence of events, including seed production, dispersal and germination, and seedling emergence, establishment and survival.

For the majority of plant species investigated in the field, the consumption of seeds prior to and following dispersal from the parent accounted for a significant proportion of plant mortality (Crawley, 1988). If the term 'predation' is used broadly to describe the behaviour of an animal that hunts, kills and consumes a food item of a

lower trophic level, such patterns of consumption may be referred to as 'pre-dispersal seed predation' and 'post-dispersal seed predation', respectively.

1.4.1.1. *Pre-dispersal seed predation*

For several consecutive years, pre-dispersal seed predators, including *Andricus quercuscalicis* (gall wasp) and *Curculio glandium* (seed weevil), were found to remove the entire seed crop of *Quercus robur* (Crawley, 1987b, cited in Crawley, 1988). Gardner (1977) recorded up to seventy-five percent pre-dispersal loss of *Fraxinus excelsior* seeds attributable to infestation by the moth, *Pseudargyrotoza conwagana*. Although invertebrates are more often responsible for pre-dispersal seed predation (Sheppard *et al.*, 1994; Clark, 1992), birds (Galetti, 1993) and mammals (Janzen, 1971; Peres, 1991; Gurnell, 1993) may also significantly contribute to early seed loss. *Sciurus variegatoides* (common variegated squirrel), for example, consumed up to eighty per cent of *Pinus flexilis* (limber pine) cones prior to opening (Benkman *et al.*, 1984). In the absence of pre-dispersal seed predation, seventy per cent of cones opened on trees.

Since most unripe fruit contain toxic and anti-nutritional compounds that are distasteful and unpalatable to herbivores (Mabberley, 1992) and the majority of tree canopy fruit are inaccessible to ground-dwelling herbivores, greater proportions of seeds are consumed after ripening and dispersal. Pre-dispersal seed predation is less widespread in temperate woodland than in tropical forests, where specialist herbivores detoxify secondary compounds and account for considerable pre-dispersal losses (Mabberley, 1992).

1.4.1.2. *Post-dispersal seed predation*

Previous studies have frequently reported high rates of post-dispersal seed predation attributable to vertebrates and invertebrates (Chapter 3). Although post-dispersal seed predators often depleted the entire seed supply, seed loss typically varied according to plant, predator and habitat characteristics, including seed density, plant species, seed burial, vegetation cover, predator density and the availability of alternative food items (Hulme, 1993). On a theoretical basis, seed loss may have a significant impact on an even-aged, isolated population of semelparous plants without a seed bank, whereas a mixed-age population of long-lived iteroparous plants with a seed bank may be less critically dependent on current reproduction (Crawley, 1983).

1.4.1.3. *Seedling herbivory*

Seeds that survive pre- and post-dispersal predation may be subject to alternative mortality factors, may persist in a bank of dormant seeds or may germinate, assuming favourable conditions. It has long been recognised that seedlings are particularly vulnerable to herbivory, which may devastate emerging populations.

"*...on a piece of ground three feet long and two wide, dug and cleared, and where there could be no choking from other plants, I marked all the seedlings of our native weeds as they came up, and out of the 357 no less than 295 were destroyed , chiefly by slugs and insects*" Darwin (1859, cited in Begon *et al.*, 1990).

Vertebrate herbivores may be up to one hundred per cent effective in destroying plant seedlings (Chapter 5), which may result in species loss if herbivores are sufficiently selective and seedlings sufficiently scarce (Crawley, 1988). Consistent with seed predation, rates of seedling herbivory may vary significantly according to plant, predator and habitat characteristics.

1.5. STUDY AIMS

The natural regeneration of many temperate woodland species has been found to be limited in many areas (Watt, 1919, 1923; Bramble & Goddard, 1942; Linhart & Whelan, 1980) or may have occurred only intermittently in the past (Peterken, 1966; Peterken & Tubbs, 1965; Ross *et al.*, 1970). However, the precise mechanisms that regulate plant recruitment, and ultimately plant distribution, community composition and species diversity, are poorly understood.

Extensive investigation has established that herbivores significantly influence plant performance, herbivores are most likely to bring about plant mortality at seed and seedling stages and herbivores often consume large quantities of seeds and seedlings. It is also recognised, however, that herbivores are unlikely to influence plant demography when plants regenerate by vegetative expansion or satiate seed predators with mast seed crops (Jensen, 1982), when banks of dormant seeds or the repeated, prolonged reproduction of long-lived iteroparous species compensate for seed and seedling loss to herbivores (Crawley, 1983), or when plant recruitment is microsite-limited rather than seed- or herbivore-limited (Hulme, 1996a).

Therefore, previous studies that quantify rates of seed or seedling predation do not alone constitute evidence that herbivores influence plant demography. The impact of herbivores on plant recruitment, and ultimately plant distribution, community composition and species diversity, can only be assessed if patterns of seed and seedling predation are considered in the broader context of the regeneration sequence (Shaw, 1968a,b). Such an investigation should also consider natural patterns of seed production, viability, dispersal and germination, and seedling emergence, establishment and survival.

The present study aimed to assess the relative impact of post-dispersal seed predation, seedling herbivory and regeneration microsite on the natural regeneration dynamics of tree species in temperate deciduous woodland. This aim was addressed through research that had the following more specific aims. These were to:

1. Describe the composition and spatial association of representative tree species in representative temperate deciduous woodland and assess patterns of past regeneration.

Chapter 2 includes general descriptions of study sites and study species. Detailed descriptions of tree populations were based on systematic sampling methods to determine the identity, density, dispersion and size distribution of saplings and adults of each tree species.

2. Quantify post-dispersal seed predation and identify primary sources of variation.

Chapter 3 describes field-based predation trials in which seeds of each species were presented at feeding depots with controlled predator access. Variation in seed removal according to tree species, predator group, microhabitat and site, and the association between rates of removal and seed characteristics, were assessed.

3. Examine the relationship between seed dispersal and post-dispersal seed predation.

Chapter 4 describes field-based predation trials designed to test the hypothesis that dispersed seeds may escape disproportionately high offspring mortality beneath parent plants resulting from increased herbivore activity. Variation in seed removal

according to seed density, distance from the parent, tree species and predator group was assessed.

4. Quantify seedling herbivory and identify primary sources of variation.

Chapter 5 describes field-based predation trials in which seedlings of each species were presented at feeding depots with controlled predator access. Variation in seedling herbivory according to tree species, predator group and microhabitat, and the association between rates of herbivory and seedling characteristics, were assessed.

5. Quantify viable seed output and natural seedling dynamics to assess the extent of current regeneration.

Chapter 6 describes vegetation surveys in which natural seed production, seedling density, seedling survival, and ground layer cover were estimated. Variation between tree species and the association between seedling recruitment and habitat characteristics was assessed.

CHAPTER 2

STUDY SITES AND STUDY SPECIES

2.1 GENERAL DESCRIPTION OF STUDY SITES

The fieldwork and experiments described in this thesis were conducted between May 1995 and December 1997 in two semi-natural deciduous woodlands in County Durham, Northeast England. Sites with the greatest species and habitat diversity, least human disturbance and active management, and fewest colonised and introduced species, were selected to best represent intact temperate deciduous woodland. These woodlands were acknowledged as an integral part of the British woodland system (Ratcliffe, 1977) and recognised as Sites of Special Scientific Interest (SSSI) under the Wildlife and Countryside Act of 1981. Vegetation communities have been described by the Nature Conservancy Council and categorised by Graham (1988). National Vegetation Classification (NVC) (Rodwell, 1991) coding and nomenclature was used when known, otherwise local code numbers and names were used. Throughout, plant species nomenclature follows Clapham *et al.* (1987).

2.1.1 **Shipley Wood**

Shipley Wood is the most southern region of the Shipley and Great Woods SSSI, situated in the district of Teesdale, County Durham (Figures 2.1 and 2.2, Plate 2.1) and ranging in altitude from 170 to 230m a.s.l. The site was first notified in 1975 under the National Parks and Access to the Countryside Act (1949). Lining the steep sandstone, limestone and gritstone banks of the River Tees, the site supports one of the most extensive (63.35 ha), diverse and pristine deciduous woodlands in Northeast England. The biological diversity and structure of the site are most indicative of ancient woodland, although additional species are represented.

On base-rich soils, *Acer pseudoplatanus* (sycamore), *Fraxinus excelsior* (ash) and *Ulmus glabra* (wych elm) dominate mature 'mixed deciduous canopies' (WOC6), overlying a discontinuous understorey containing *Crataegus monogyna* (hawthorn), *Ilex aquifolium* (holly), *Prunus padus* (bird cherry) and coppiced *Corylus avellana* (hazel). The field layer contains a rich assemblage of woodland species, characteristic of a '*Fraxinus-Acer campestre-Mercurialis* woodland' of the '*Ranunculus ficaria-Anemone* sub-community' (WO6 / NVC8b). Common herb species include

Figure 2.1. Location of study sites in County Durham

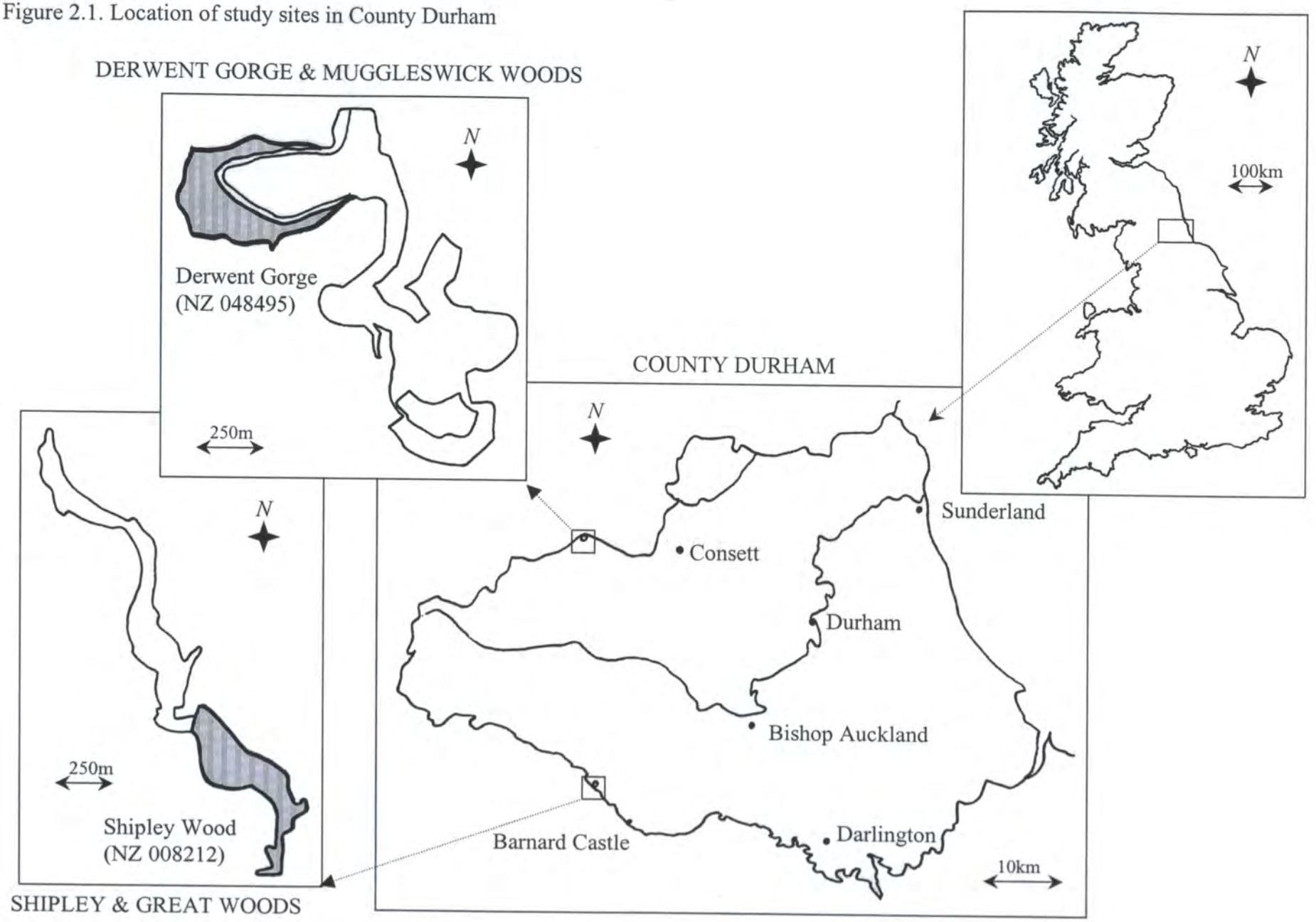


Figure 2.2. Schematic diagram of Shipley Wood, showing position of upper (U), middle (M) and lower (L) transects.

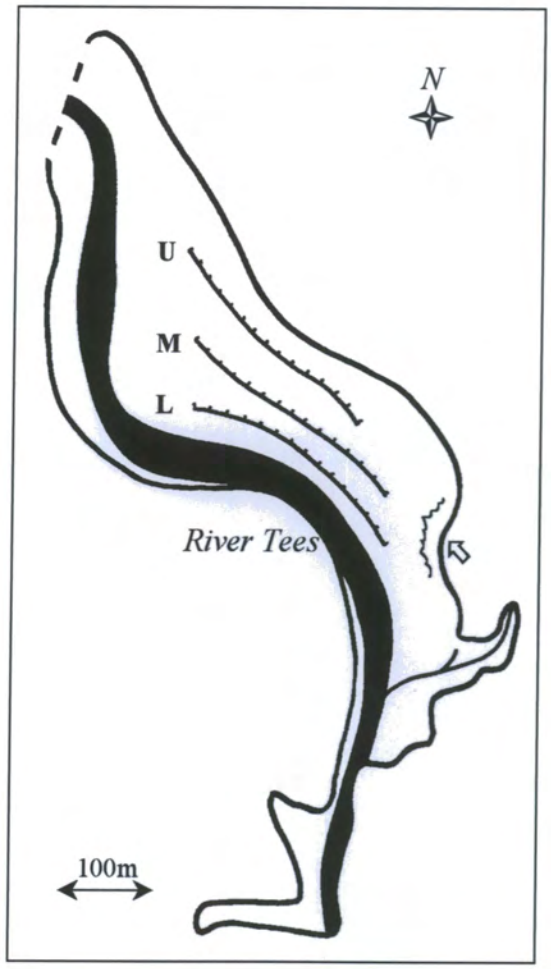


Plate 2.1. North-westward view over Shipley Wood, from position marked ↖ in Figure 2.2

Mercurialis perennis (dog's mercury), *R. ficaria* (lesser celandine), *Filipendula ulmaria* (meadowsweet), *Geum urbanum* (wood avens), *Galium aparine* (cleavers), *Oxalis acetosella* (wood-sorrel) and *Circaea lutetiana* (enchanter's-nightshade).

Alnus glutinosa (alder) dominates locally on flushed soils, with *Allium ursinum* (ramsons) and *Chrysosplenium oppositifolium* (opposite-leaved golden-saxifrage) in the field layer. On dry acidic soils, *Quercus petraea* (sessile oak) and *Betula pendula* (silver birch) dominate over a field layer containing *Deschampsia flexuosa* (wavy hair-grass), *Luzula sylvatica* (great wood-rush) and *Melampyrum pratense* (common cow-wheat). *Taxus baccata* (yew) occurs sporadically throughout the site, often restricted to steep slopes and wooded outcrops. Fern species, including *Dryopteris filix-mas* (male fern) and *Pteridium aquilinum* (bracken), dominate locally beneath open canopies.

Shipley and Great Woods also support over one hundred moss and liverwort species, and the richest assemblage of epiphytic lichens in Northeast England, including many nationally and regionally rare species and the first definite British record of *Baccidia affinis* (Ratcliffe, 1977). Other relict ancient woodland species include *Lobaria pulmonaria*, *L. laetevirens*, *Pachyphiale cornea*, *Catillaria sphaeroides* and *Bacidia epixanthoides*.

Human disturbance was minimal due to the private ownership, remoteness, restricted public access and limited management of the site. English Nature was not involved in any active management of the site during the study period. However, the site was occasionally used for game shooting, annually between September and January, and consequently contained a small number of grain feeders. Adjacent land was principally used as grazing pasture for sheep and cattle.

2.1.2 **Derwent Gorge**

Derwent Gorge is the most northern region of the extensive (93.75 ha) Derwent Gorge and Horsleyhope Ravine SSSI, situated in the district of Derwentside, County Durham (Figures 2.1 and 2.3, Plate 2.2) and ranging in altitude from 175 to 245m a.s.l. The site was first notified in 1976 under the National Parks and Access to the Countryside Act (1949). Situated on the steep slopes and crags of a ravine cut by the River Derwent, the site supports a diversity of primary and ancient woodland species.

Figure 2.3. Schematic diagram of Derwent Gorge, showing location of upper (U), middle (M) and lower (L) transects.

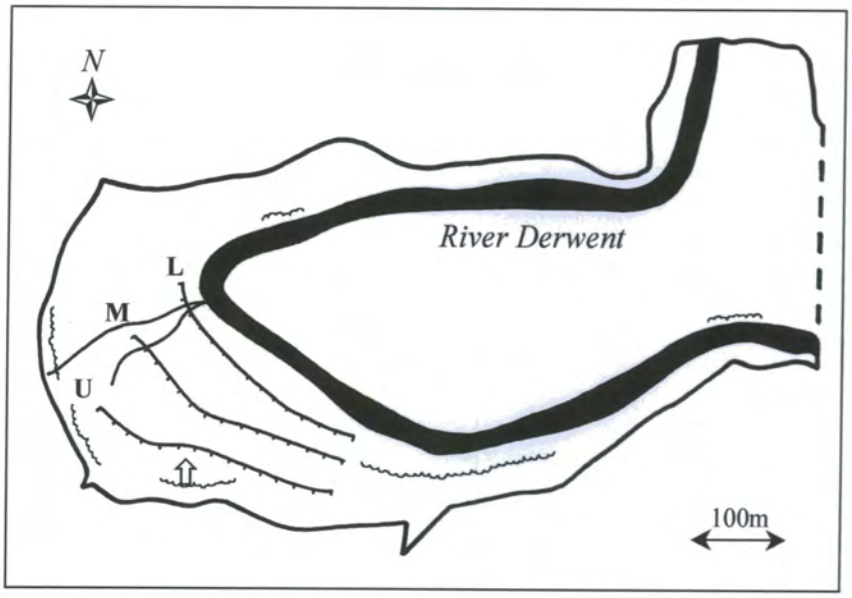


Plate 2.2. Northward view over Derwent Gorge, from position marked ⇧ in Figure 2.3

Dry, acidic soils support an 'oak/birch canopy' (WOC1, WOC2) of *Q. petraea* and *B. pendula*, overlying an understorey of *Sorbus aucuparia* (rowan) and *I. aquifolium*. The rich ground flora is characteristic of a '*Q. petraea-Betula pubescens-Dicranum majus* woodland' of the '*Anthoxanthum-Agrostis capillaris* sub-community' (WO25 / NVC17c, WO27 / NVC17c). *L. sylvatica*, *D. flexuosa*, *O. acetosella* and *Vaccinium myrtillus* (bilberry) dominate the field layer, while *Anthoxanthum odoratum* (sweet vernal-grass), *P. aquilinum*, *M. pratense*, *Viola riviniana* (common dog-violet) and *Potentilla erecta* (tormentil) are frequent.

Moist, base-rich soils support 'alder/willow carr and damp woodland canopies' (WOC9). On drier slopes, *A. pseudoplatanus*, *F. excelsior*, *Q. petraea* and *U. glabra* compose the mixed canopies, overlying a discontinuous understorey containing *C. avellana* and *P. padus*, with *Fagus sylvatica* (beech) locally dominant. *M. perennis*, *Urtica dioica* (common nettle), *C. lutetiana*, *Ajuga reptans* (bugle), *F. ulmaria*, *G. urbanum*, *G. aparine* and *Veronica montana* (wood speedwell) are common in the field layer. On flushed riverbank soils, mixed canopies grade to stands of *A. glutinosa*, with *A. ursinum*, *C. oppositifolium*, *Ranunculus repens* (creeping buttercup), *Juncus effusus* (soft rush) and *Veronica beccabunga* (brooklime) in the field layer. *T. baccata* occurs sporadically throughout the site, almost entirely restricted to severe slopes and wooded crags.

Derwent Gorge and Horsleyhope Ravine also support a rich assemblage of more than sixty epiphytic woodland lichens, including regionally rare species (*Cyphelium inquinans*) and species indicative of long established woodland (*Pachyphiale cornea* and *Thelotrema lepadinum*).

Human disturbance was minimal due to the private ownership, remoteness, restricted public access and limited management of the site. The activities of English Nature were principally concerned with the control of *A. pseudoplatanus* and *F. sylvatica*. The site was occasionally used for game shooting, annually between September and January, and consequently contained a small number of anti-predator snares. Adjacent land was principally used for cultivation and grazing pasture for sheep and cattle.

2.2 GENERAL DESCRIPTION OF STUDY SPECIES

A range of tree species was selected to best represent the diversity of natural regeneration in temperate deciduous woodland, according to the following criteria.

1. Species were characteristic of mixed temperate deciduous woodland and present in both study sites.
2. Species represented canopy and understorey tree populations that differed in density within and between study sites.
3. Species differed in regenerative and dispersal characteristics, and the timing of flowering, seed set and germination.

The study principally investigated the regeneration of the native, established tree species *B. pendula*, *F. excelsior*, *I. aquifolium*, *S. aucuparia*, *T. baccata* and *U. glabra*. It was subsequently necessary to modify the experimental design to include the colonising species, *A. pseudoplatanus*.

The study species were particularly common of mixed woodland sites, representing a diversity of ecological attributes, as summarised in Table 2.1. *Acer*, *Betula*, *Fraxinus*, *Sorbus* and *Ulmus* are deciduous trees, whereas, *Ilex* and *Taxus* are evergreen. In both study sites, *Acer*, *Betula* and *Fraxinus* were components of high canopy, whereas *Ilex*, *Sorbus*, *Taxus* and *Ulmus* were components of low canopy or understorey vegetation. Established strategies include competitors (*Fraxinus* and *Ulmus*), stress-tolerant competitors (*Ilex* and *Sorbus*) and intermediates between competitors and stress-tolerant competitors (*Acer* and *Betula*) (Grime *et al.*, 1988).

All taxa principally regenerate by seed, either with an abundance of wind-dispersed seed (*Acer*, *Betula*, *Fraxinus* and *Ulmus*) or by seasonal regeneration into vegetation gaps from animal dispersed seed (*Ilex*, *Sorbus* and *Taxus*) (Grime *et al.*, 1988). There is some evidence that *Ilex* achieves vegetative expansion when leafy stems detached by herbivores root when covered by moist litter (Peterken & Lloyd, 1967). Although vegetative spread may be locally important in colonising canopy gaps, along with regeneration involving a bank of persistent seedlings, it is ineffective as a mechanism of dispersal.

Flowering and fruiting periods also varied between tree species. For example, *Ulmus* may flower as early as February and fruit as early as May, for immediate germination and summer growth. In contrast, *Ilex* may flower as late as August and fruit as late as the following March. Whereas seeds of *Acer*, *Betula* and *Sorbus*

Table 2.1. Comparative ecological attributes of each study species (Tansley, 1939; Jones, 1945; Wardle, 1959, 1961; Webb & Glanville, 1962; Peterken, 1966; Peterken & Lloyd, 1967; Linhart & Whelan, 1980; Rose, 1981; Gill & Davy, 1983; Pigott, 1983; Evans, 1988; Grime *et al.*, 1988; Morgan, 1991; Atkinson, 1992; Tapper, 1992; Peltier *et al.*, 1997; Emborg, 1998). Regenerative strategies include regeneration by numerous wind-dispersed seeds or spores (W), seasonal regeneration in vegetation gaps (S), vegetative expansion (V) and regeneration involving a bank of persistent seedlings (B) (Grime *et al.*, 1988). Established strategies include competitor (C) and stress-tolerant competitor (SC) (Grime *et al.*, 1988).

Taxon	General description	Geographical distribution	Habitats	Established strategy	Regenerative strategy	Flowering period	Fruiting period
Acer	Deciduous, monoecious tree of up to 30m height.	Native to mountains of S and C Europe and Asia; widely planted and naturalised throughout Britain and lowlands of C and N Europe.	Widespread, particularly woodland habitats.	C/SC	W	April to June	September to November
Betula	Deciduous, monoecious tree of up to 25m height.	N and C Europe, and locally on mountains of S Spain; temperate Asia and Britain, particularly N and W. Occasionally naturalised.	Widespread, particularly scrub, woodland and rocky open habitats. Absent from hedgerows, pasture, disturbed and aquatic habitats.	C/SC	W	April to July	September onwards
Fraxinus	Deciduous tree of up to 35m height, with hermaphrodite or separate sex flowers.	Britain, except parts of Scottish Highlands; Europe, except N, S and E margins; N Africa and W Asia.	Widespread in all but aquatic habitats, particularly woodlands, hedgerows, meadows, shaded river banks, lead-mine spoil and scree.	C	W	April to May	September onwards
Ilex	Evergreen, dioecious tree or shrub of 3-15m height (rarely 20m). Occasionally sterile.	Britain, common throughout, except C; Europe, particularly W, rarer E.	Widespread in woodland, scrub and hedgerows.	SC	S (V,B)	May to August	September to March
Sorbus	Deciduous tree of up to 15m height, with hermaphrodite flowers.	Britain, but rare in C and E England; Europe; N Asia.	Mainly restricted to wooded sites, but also on skeletal habitats, including wasteland and lead mines.	SC	S	May to June	September to October
Taxus	Evergreen, dioecious tree or shrub of 10-25m height.	Restricted distribution in Britain, with local dominance only in S England; more widespread throughout Europe	Grows on a wide variety of soils and substrates, typically in scrub and woodland.		S	February to April	August to September
Ulmus	Deciduous tree of 25-40m height, with hermaphrodite flowers.	Britain, particularly N and W; Europe, except extreme N and S; W Asia and N Africa.	Widespread, particularly spoil and rocky habitats, limestone woodland and scrub. Absent from grassland and aquatic habitats	C	W	February to April	May to July

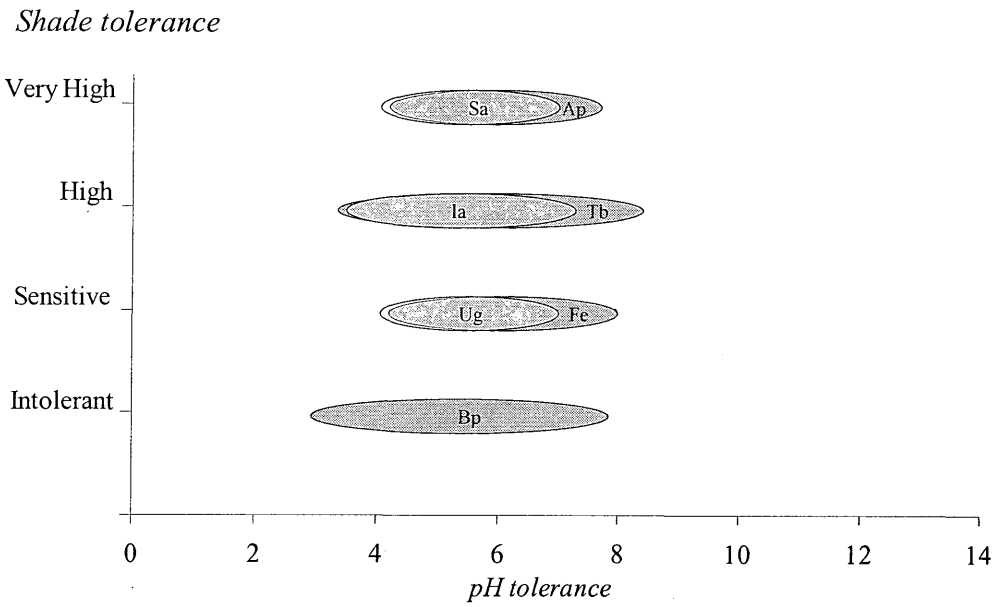
Table 2.1. Continued.

Taxon	Primary seed dispersal	Germination	pH tolerance	Shade tolerance	Soil moisture	Tolerance of seedlings Competition	Tolerance of seedlings Climate	Life span
Acer	Short distance wind dispersed	January to Spring, synchronous after chilling.	Widely distributed (pH 4.15-7.6), frequently on base-rich soils.	Very high, decreasing with age	Sensitive to drought on shallow soils	Intolerant of herb competition	Low tolerance of late frost	400-600 years (in open stands)
Betula	Long distance wind dispersed	Spring, after chilling.	Widely distributed (pH 3.0-7.8), frequently on acidic soils.	Intolerant	Intolerant of drought	Low tolerance	Cold tolerant	≈60-70 years
Fraxinus	Wind dispersed	Usually in 2nd spring following seed set, after chilling.	Widely distributed (pH 4.2-8.0), frequently on base-rich soils.	Sensitive, may limit recruitment	Sensitive to drought on shallow soils	Sensitive to herb and intraspecific competition	Sensitive to late frost	≈180 years (>300 years if coppiced)
Ilex	Animal dispersed	Usually in 2nd or 3rd spring following seed set, after scarification and chilling	Widely distributed (pH 3.5-7.2), frequently on acidic soils.	High, but growth limited	Intolerant of drought or prolonged waterlogging		Sensitive to late frost	250-300 years
Sorbus	Animal dispersed	Spring, after chilling	Widely distributed (pH 4.0-7.0), frequently on acidic soils.	Very high				Up to 150 years
Taxus	Animal dispersed	Usually in 2nd or 3rd spring following seed set, after scarification and chilling	Widely distributed (pH 3.4-8.4), frequently on base-rich soils.	High, but growth and flowering limited			Sensitive to cold stress on exposed sites.	May exceed 1000 years
Ulmus	Long distance wind dispersed	Immediate, following summer shedding.	Widely distributed (pH 4.0-7.0), frequently on base-rich soils.	Sensitive, may limit recruitment	Intolerant of drought			Often >200 years

usually germinate in the spring following seed set, seeds of *Fraxinus*, *Ilex* and *Taxus* delay germination until the second or third spring. With the exception of *Ulmus*, seed germination requires a period of chilling, while the germination of *Ilex* and *Taxus* seeds is improved by scarification.

The study species also differ in their environmental requirements and tolerances. Although all taxa are widely distributed on a variety of soil types and substrates, *Acer*, *Fraxinus*, *Taxus* and *Ulmus* are prevalent on more basic soils, whereas *Betula*, *Ilex* and *Sorbus* are prevalent on more acidic soils. *Betula* and *Taxus* have particularly broad pH tolerances, the latter having been recorded on acidic mor humus soils down to pH 3.4 (Webb & Glanville, 1962) and basic limestone soils up to pH 8.4 (Tansley, 1939). *Acer*, *Ilex*, *Sorbus* and *Taxus* are highly shade tolerant, whereas *Betula*, *Fraxinus* and *Ulmus* are either sensitive or intolerant of shade. Although differences in shade- and pH-tolerance account for some degree of niche partitioning between study species (Figure 2.4), alternative factors are likely to explain further dispersion, particularly between taxa that share similar shade- and pH-tolerances (*Acer-Sorbus*, *Ilex-Taxus* and *Fraxinus-Ulmus*).

Figure 2.4. The dispersion of study species according to shade- and pH-tolerance (Table 2.1). Taxa include *Acer* (Ap), *Betula* (Bp), *Fraxinus* (Fe), *Ilex* (Ia), *Sorbus* (Sa), *Taxus* (Tb) and *Ulmus* (Ug). pH tolerances are represented as ranges.



The species for which data are available also exhibit varying degrees of sensitivity to waterlogging, drought stress, competition and cold stress. Once

established, the life spans of adult trees differ markedly between species. Adults of *Betula* may survive for only 60-70 years, whereas adults of *Taxus* may survive for more than one thousand years. Alternative regeneration processes most likely support contrasting population dynamics.

2.3 DETAILED DESCRIPTION OF TREE POPULATIONS

2.3.1 **Materials and methods**

Each site was surveyed systematically using three equidistant linear transects traversing upper, middle and lower regions of the site, each with fifteen survey points at twenty metre intervals (Figures 2.2 and 2.3). At each survey point, the composition, density and canopy area of adult trees (height ≥ 3m, basal girth ≥ 10cm) were estimated using the 'point-centred quarter' method (Cottam *et al.*, 1953).

The density of saplings (30cm<height<3m, 1cm<basal girth<10cm) of each study species within a 10m x 10m quadrat at each point, was recorded. The density of adult *Ilex* within quadrats was also recorded for population estimates, since sparse individuals of this species were not encountered during point-centred quarter sampling. In addition, the size distribution and spatial association of adult populations were determined from the basal girth and distance to nearest conspecific adult of thirty individuals of each species. Spatial associations were interpreted according to the Clark & Evans (1954) index;

$$R = r_A / r_E$$

where r_A is the observed mean nearest neighbour distance from a random individual, and r_E is the expected mean distance, assuming a random distribution.

$$r_E = \frac{1}{2\sqrt{d}}$$

where d is the population density. If individuals are randomly distributed the expectation is unity, whereas aggregation is indicated by low values of R and regularity by high values. Values range from zero, with maximum aggregation, to 2.1491 when the distribution is perfectly regular. The significance of the departure of r_A from r_E can be determined using the formula;

$$c = \frac{r_A - r_E}{\sigma r_E}$$

where c is the standard variate of the normal curve. σr_E is the standard error of the mean distance to the nearest neighbour in a randomly distributed population of the same density as that of the observed population. The value of σr_E for a population density of d is;

$$\sigma r_E = \frac{0.26136}{\sqrt{Nd}}$$

where N is the number of measurements of distance made. The c values of 1.96 and 2.58 represent the 5% and 1% levels of significance, respectively, for a two-tailed test.

Five replicate soil samples were taken at intervals from each transect (upper, middle and lower) of each study site for the determination of soil pH. For each sample, 10g of sieved (2mm mesh) soil was stirred into 25ml of distilled water and allowed to stand for thirty minutes. A pH measurement was then taken using an electrode calibrated at pH 4.0 and pH 7.0. Since pH was equal to the negative logarithm of the concentration of hydrogen ions, pH measurements were converted to hydrogen ion concentrations for analysis. Variation in soil pH between transects and sites was determined statistically using analysis of variance.

2.3.2 **Results**

2.3.2.1 *Composition, density and canopy basal area of adult tree populations*

With the exception of *Fagus sylvatica*, which was absent from Shipley Wood, the same tree species were represented in both study sites (Table 2.2). Mean canopy basal area was also similar between Shipley Wood and Derwent Gorge, with consistent patterns of increasing basal area from upper to lower slopes. The density and distribution of adult trees did vary between species, between sites and within sites. The total density of all tree species was more than twice as great in Shipley Wood than in Derwent Gorge. In both sites, *Acer*, *Fraxinus* and *Corylus* were at a high relative density and *Ilex*, *Prunus*, *Salix*, *Sambucus*, *Taxus* and *Ulmus* were at a low relative density. *Alnus*, *Betula* and *Crataegus* were more characteristic of Shipley Wood, whereas *Fagus*, *Quercus* and *Sorbus* were more characteristic of Derwent Gorge.

In Shipley Wood, total tree density increased markedly from upper to lower slopes, as did the density of *Acer*, *Alnus*, *Betula*, *Corylus*, *Fraxinus*, *Ilex*, *Prunus*, *Quercus* and *Ulmus*. In contrast, *Sorbus* was restricted to middle slopes, *Sambucus* and *Taxus* were restricted to upper slopes, *Salix* was predominant on upper and lower

Table 2.2. Composition, density and canopy basal area of tree species on upper, middle and lower transects of Shipley Wood and Derwent Gorge using the point-centred quarter method. The overall density of each species and the relative density, as a proportion of total tree density, are included for each site. * Densities of *Ilex aquifolium* were estimated from 10m x 10m quadrat data.

	Adult tree density (trees ha^{-1})									
	Shipley Wood					Derwent Gorge				
Species	Upper	Middle	Lower	Mean	Relative density (%)	Upper	Middle	Lower	Mean	Relative density (%)
Acer pseudoplanatus	28.9	37.8	142.1	69.6	12.0	42.0	121.0	38.5	67.2	24.9
Alnus glutinosa	0.0	107.1	304.6	137.2	23.6	3.8	6.4	25.7	12.0	4.4
Betula pendula	26.5	56.7	182.7	88.6	15.2	7.6	19.1	3.2	10.0	3.7
Corylus avellana	0.0	6.3	203.0	69.8	12.0	30.5	25.5	35.3	30.4	11.3
Crataegus monogyna	33.7	44.1	40.6	39.5	6.8	0.0	6.4	0.0	2.1	0.8
Fagus sylvatica	0.0	0.0	0.0	0.0	0.0	7.6	0.0	32.1	13.2	4.9
Fraxinus excelsior	2.4	69.3	203.0	91.6	15.7	42.0	76.4	28.9	49.1	18.2
*Ilex aquifolium**	0.0	0.0	6.7	2.2	0.4	0.0	0.0	6.7	2.2	0.8
Prunus padus	7.2	12.6	40.6	20.1	3.5	15.3	12.7	3.2	10.4	3.8
Quercus petraea	0.0	6.3	20.3	8.9	1.5	34.3	70.1	12.8	39.1	14.5
Salix caprea	12.0	6.3	20.3	12.9	2.2	7.6	6.4	0.0	4.7	1.7
Sambucus nigra	24.1	0.0	0.0	8.0	1.4	11.4	0.0	0.0	3.8	1.4
Sorbus aucuparia	0.0	6.3	0.0	2.1	0.4	11.4	31.9	6.4	16.6	6.1
Taxus baccata	9.6	0.0	0.0	3.2	0.5	3.8	0.0	0.0	1.3	0.5
Ulmus glabra	0.0	25.2	60.9	28.7	4.9	11.4	6.4	6.4	8.1	3.0
Total density (trees ha^{-1})	144.4	378.0	1225.0	582.4		229.0	382.2	199.2	270.2	
Canopy basal area (m^2 ha^{-1})	10.2	24.3	50.5	28.3		17.8	33.4	36.6	29.3	

slopes and *Crataegus* occurred at a similar density throughout the site. In Derwent Gorge, total tree density was greatest on middle slopes, as were the densities of *Acer*, *Betula*, *Crataegus*, *Fraxinus* and *Quercus*. Consistent with Shipley Wood, *Sambucus* and *Taxus* were restricted to upper slopes, *Sorbus* was predominant on middle slopes, and *Alnus* and *Ilex* were predominant on lower slopes. *Prunus*, *Salix*, and *Ulmus* were also most abundant on upper slopes, with *Fagus* predominant on lower slopes and *Corylus* at a similar density throughout the site.

In general, the upper freely draining slopes of Shipley Wood supported a canopy dominated by *Acer* and *Betula*, with *Crataegus* and *Sambucus* in the understorey. Damper middle and lower slopes supported a mixed canopy dominated by *Acer*, *Alnus*, *Betula* and *Fraxinus*, with *Crataegus* and *Corylus* in the understorey. Dry upper slopes of Derwent Gorge supported a canopy dominated by *Acer*, *Fraxinus* and *Quercus*, with *Corylus* and *Sorbus* in the understorey, whereas damper lower slopes supported a mixed canopy dominated by *Acer*, *Alnus*, *Fagus* and *Fraxinus*, with *Corylus* in the understorey.

2.3.2.2 *Spatial association of adult tree populations*

The spatial association of adult tree populations varied between tree species and study sites (Table 2.3). In Shipley Wood and Derwent Gorge, adult trees of *Betula*, *Sorbus*, *Taxus* and *Ulmus* were spatially aggregated, whereas adults of *Fraxinus* were randomly distributed. Adult trees of *Acer* and *Ilex* were aggregated in Shipley Wood, but randomly distributed in Derwent Gorge.

Table 2.3. The spatial distribution of adult trees of each study species in Shipley Wood and Derwent Gorge, according to the Clark & Evans (1954) index. *R* reflects the departure of the observed mean nearest neighbour distance (r_A) from the expected mean nearest neighbour distance (r_E), while *p* is the probability of a greater difference between r_A and r_E. Tr_A is the mean nearest neighbour distance for each tree species across both sites, and Sr_A is the mean nearest neighbour distance for each site across all species. Significance levels (*p*) were <0.01 (✶✶) and ≥0.05 (n.s., not significant).

Taxon	Shipley Wood			Derwent Gorge			
	R	r_A (m)	Distribution (*p*)	*R*	r_A (m)	Distribution (*p*)	Tr_A (m)
Acer	0.667	4.00	AGGREGATED (✶✶)	0.994	6.06	RANDOM (n.s.)	**5.03**
Betula	0.387	2.05	AGGREGATED (✶✶)	0.270	4.27	AGGREGATED (✶✶)	**3.16**
Fraxinus	1.050	5.50	RANDOM (n.s.)	0.973	6.94	RANDOM (n.s.)	**6.22**
Ilex	0.316	10.65	AGGREGATED (✶✶)	0.974	32.84	RANDOM (n.s.)	**19.0**
Sorbus	0.205	7.06	AGGREGATED (✶✶)	0.694	8.52	AGGREGATED (✶✶)	**7.79**
Taxus	0.447	12.49	AGGREGATED (✶✶)	0.128	5.67	AGGREGATED (✶✶)	**9.08**
Ulmus	0.691	6.45	AGGREGATED (✶✶)	0.466	8.20	AGGREGATED (✶✶)	**7.33**
	Sr_A (m)	**6.24**		Sr_A (m)	**8.55**		

2.3.2.3 *Sapling recruitment and the size distribution of adult tree populations*

The absolute density of saplings and the relative density, expressed as the ratio of sapling density to adult density, varied between tree species and study sites (Table 2.4). Total sapling recruitment was greater in Shipley Wood than in Derwent Gorge, both in absolute (944.4 and 117.7 saplings ha^{-1}, respectively) and relative terms (3.3 and 0.8 saplings $adult^{-1}$, respectively). In Shipley Wood and Derwent Gorge, saplings of *Acer*, *Fraxinus* and *Ulmus* were of the greatest absolute density, whereas saplings of *Betula*, *Ilex* and *Sorbus* were infrequent. No saplings of *Taxus* were encountered in either site during the study period. The relative recruitment of *Fraxinus*, *Sorbus* and *Ulmus* saplings was considerably greater in Shipley Wood than in Derwent Gorge, whereas the relative recruitment of *Betula* saplings was greater in Derwent Gorge than in Shipley Wood. Adults and saplings of *Acer* and *Ilex* were at a similar density in both study sites.

Table 2.4. Adult density, absolute sapling density and relative sapling density for each study species in Shipley Wood and Derwent Gorge.

	Shipley Wood			Derwent Gorge		
Taxon	Adult density (ha^{-1})	Sapling density Absolute (ha^{-1})	Relative ($adult^{-1}$)	Adult density (ha^{-1})	Sapling density Absolute (ha^{-1})	Relative ($adult^{-1}$)
Acer	69.6	80.0	1.15	67.2	66.7	0.99
Betula	88.6	2.2	0.02	10.0	4.4	0.44
Fraxinus	91.6	775.6	8.47	49.1	33.3	0.68
Ilex	2.2	2.2	1.00	2.2	2.2	1.00
Sorbus	2.1	13.3	6.33	16.6	0.0	0.00
Taxus	3.2	0	0.00	1.3	0.0	0.00
Ulmus	28.7	71.1	2.48	8.1	11.1	1.37
Total	286.0	944.4	3.30	154.5	117.7	0.76

The mean basal girths of adult *Acer*, *Betula*, *Sorbus* and *Ulmus* were similar between sites, whereas the mean girths of adult *Fraxinus* and *Ilex* were greater in Derwent Gorge than in Shipley Wood and the mean girth of adult *Taxus* was greater in Shipley Wood than in Derwent Gorge (Table 2.5). The size distribution of adult tree populations also varied between tree species and study sites (Figures 2.5-2.11). For the majority of tree populations, the density of saplings and adults of low girth was greater than or similar to the density of adults of high girth. Such patterns were consistent with current regeneration and a continuum of past regeneration. However, saplings of *Sorbus* and *Taxus* in Derwent Gorge and *Betula* in Shipley Wood were either absent or infrequent, and adults of lowest girth were proportionally less abundant than those of intermediate girth. Limited recent regeneration was most pronounced for *Taxus* in Shipley Wood, where saplings and adults of lowest girth were absent and populations consisted entirely of high girth adults. Hulme (1996a) recorded similar unimodal age-distribution patterns within *Fraxinus-Acer* woodlands in County Durham, with peak regeneration occurring between 150 and 200 years ago, reflecting microsite- and herbivore-limited current recruitment. High girth adults of *Ilex* and *Ulmus* were absent in Shipley Wood, where populations consisted entirely of saplings and low girth adults. Such patterns reflected either limited past regeneration or restricted maximum adult girth, as determined by the habitat characteristics of each study site.

Table 2.5. Mean basal girth (cm) of each study species in Shipley Wood and Derwent Gorge. Standard errors and results of t-tests for variation between sites, are included.

	Shipley Wood		Derwent Gorge				
Taxon	Mean	S.E.	Mean	S.E.	t	df	*p*
Acer	92.1	12.6	88.9	8.8	0.209	52	n.s.
Betula	90.5	6.8	80.6	10.3	-0.801	50	n.s.
Fraxinus	64.7	9.0	161.4	15.4	5.423	47	***
Ilex	42.3	3.5	104.6	12.7	4.714	28	***
Sorbus	56.5	7.3	67.5	5.9	-1.179	58	n.s.
Taxus	222.3	9.2	116.6	11.0	-7.376	58	***
Ulmus	46.2	4.0	66.6	10.5	1.817	37	n.s.

Figure 2.5. The log density (± 1 S.E.) of *Acer* saplings (basal girth<10cm) and the size distribution of adult tree populations in Shipley Wood and Derwent Gorge.

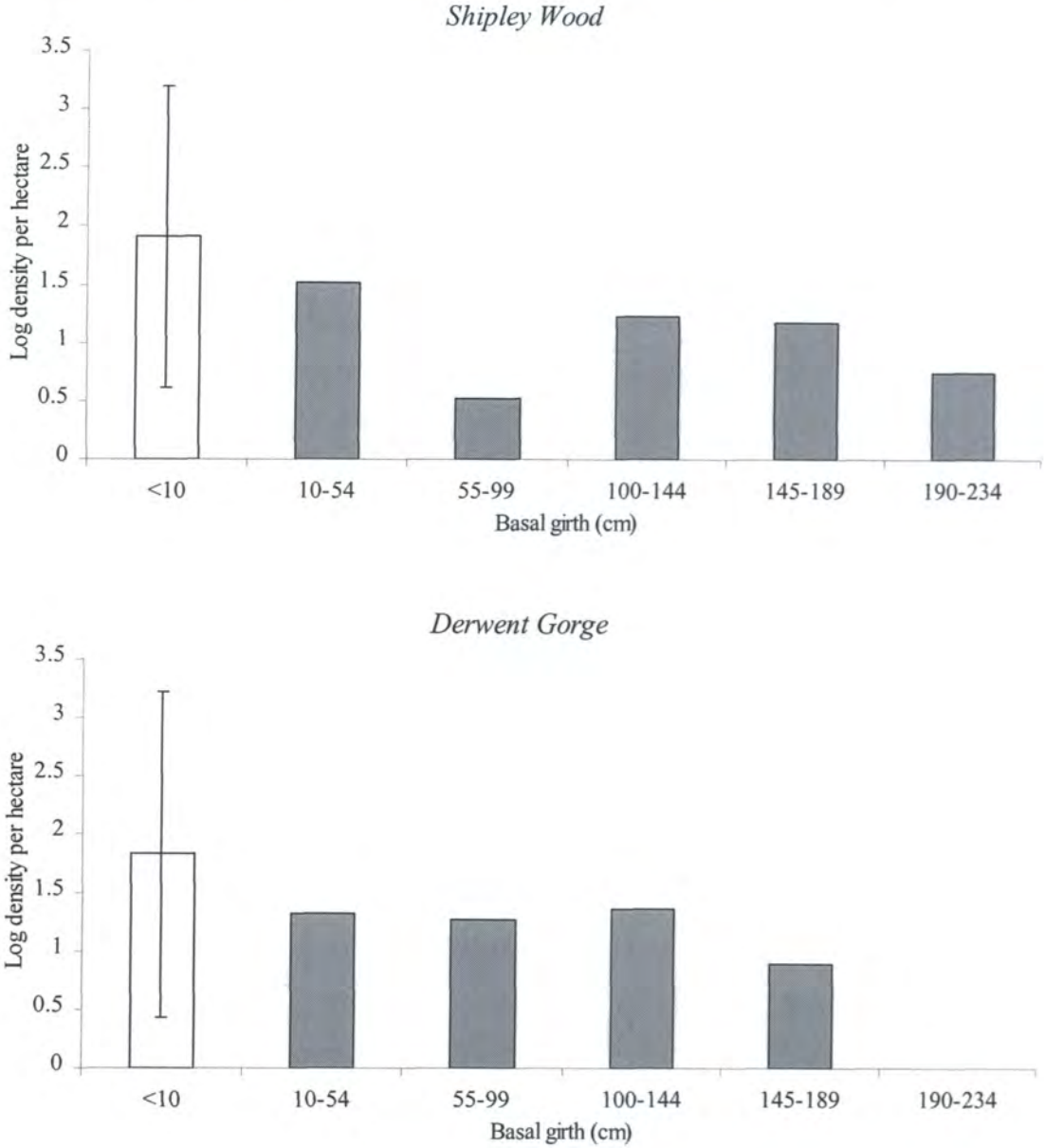


Figure 2.6. The log density (± 1 S.E.) of *Betula* saplings (basal girth<10cm) and the size distribution of adult tree populations in Shipley Wood and Derwent Gorge.

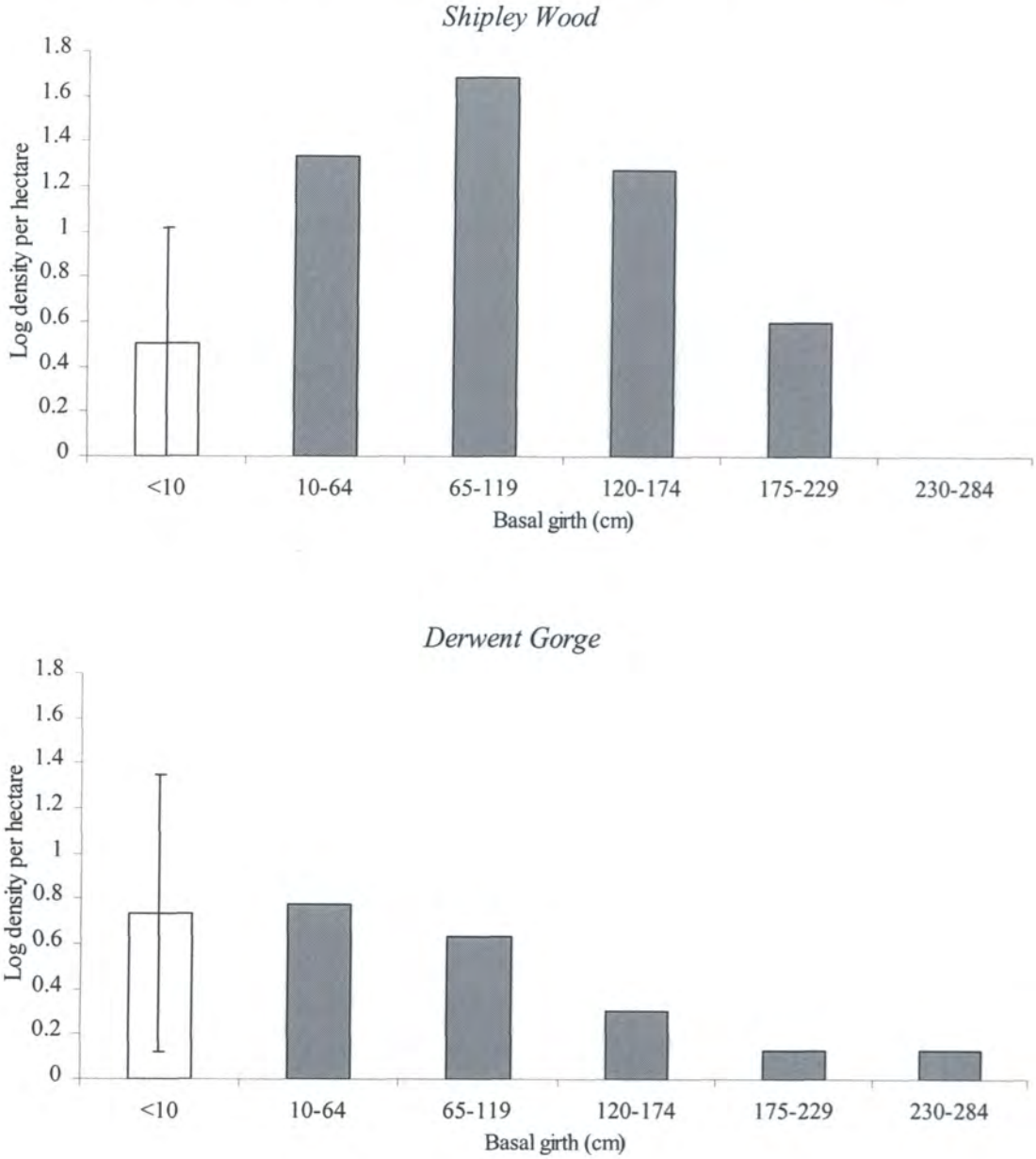


Figure 2.7. The log density (± 1 S.E.) of *Fraxinus* saplings (basal girth<10cm) and the size distribution of adult tree populations in Shipley Wood and Derwent Gorge.

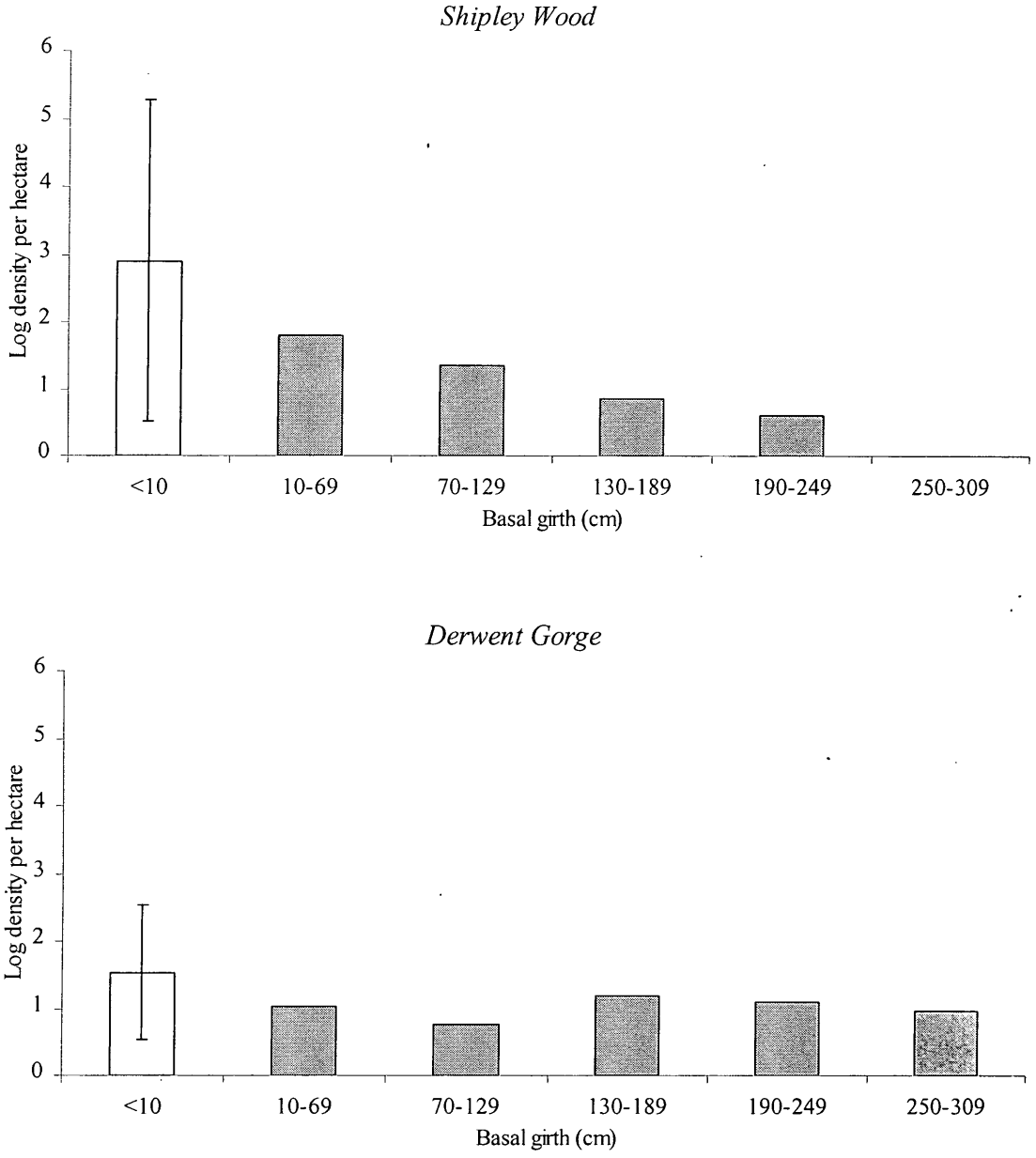


Figure 2.8. The log density (± 1 S.E.) of *Ilex* saplings (basal girth<10cm) and the size distribution of adult tree populations in Shipley Wood and Derwent Gorge.

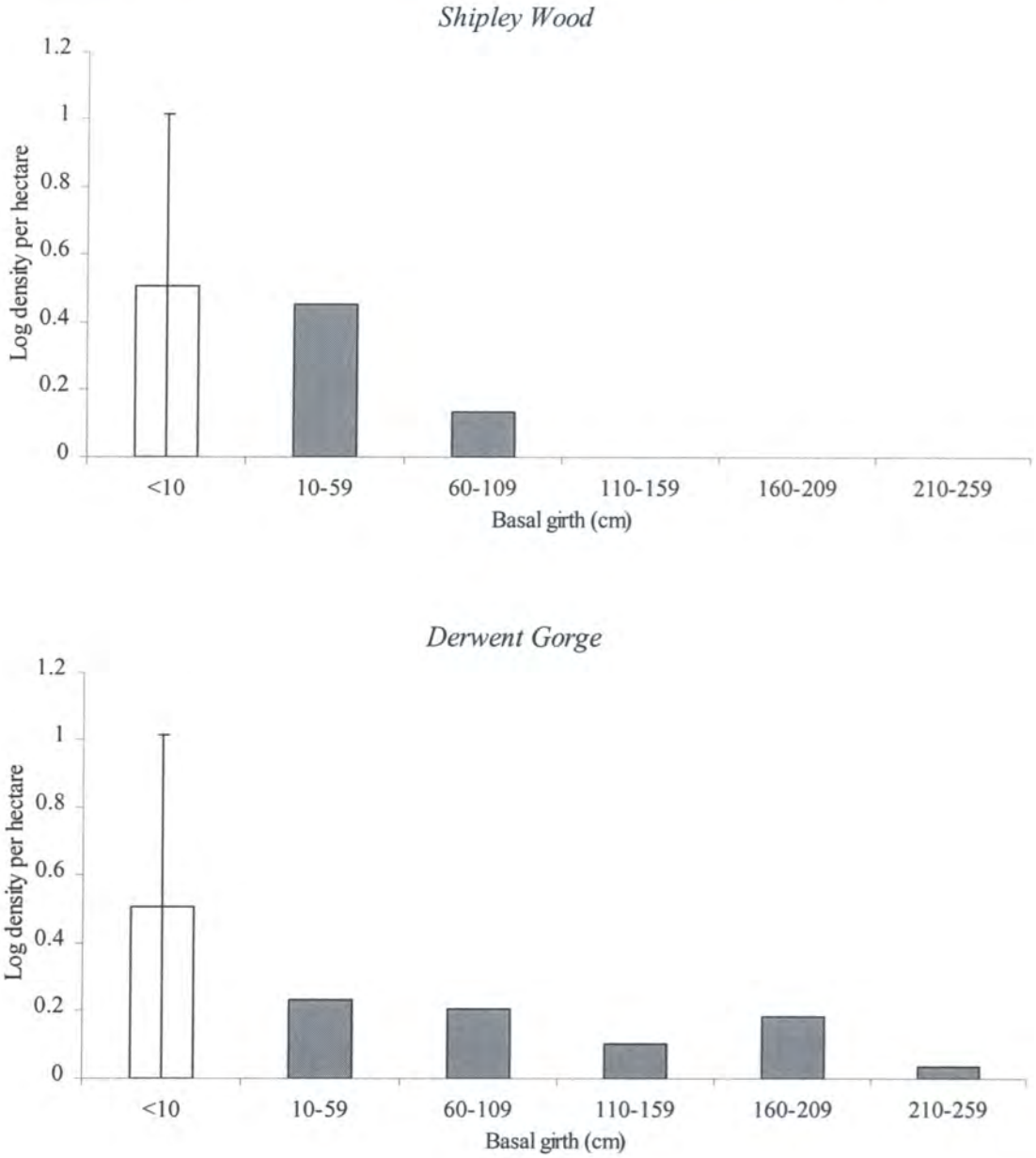


Figure 2.9. The log density (± 1 S.E.) of *Sorbus* saplings (basal girth<10cm) and the size distribution of adult tree populations in Shipley Wood and Derwent Gorge.

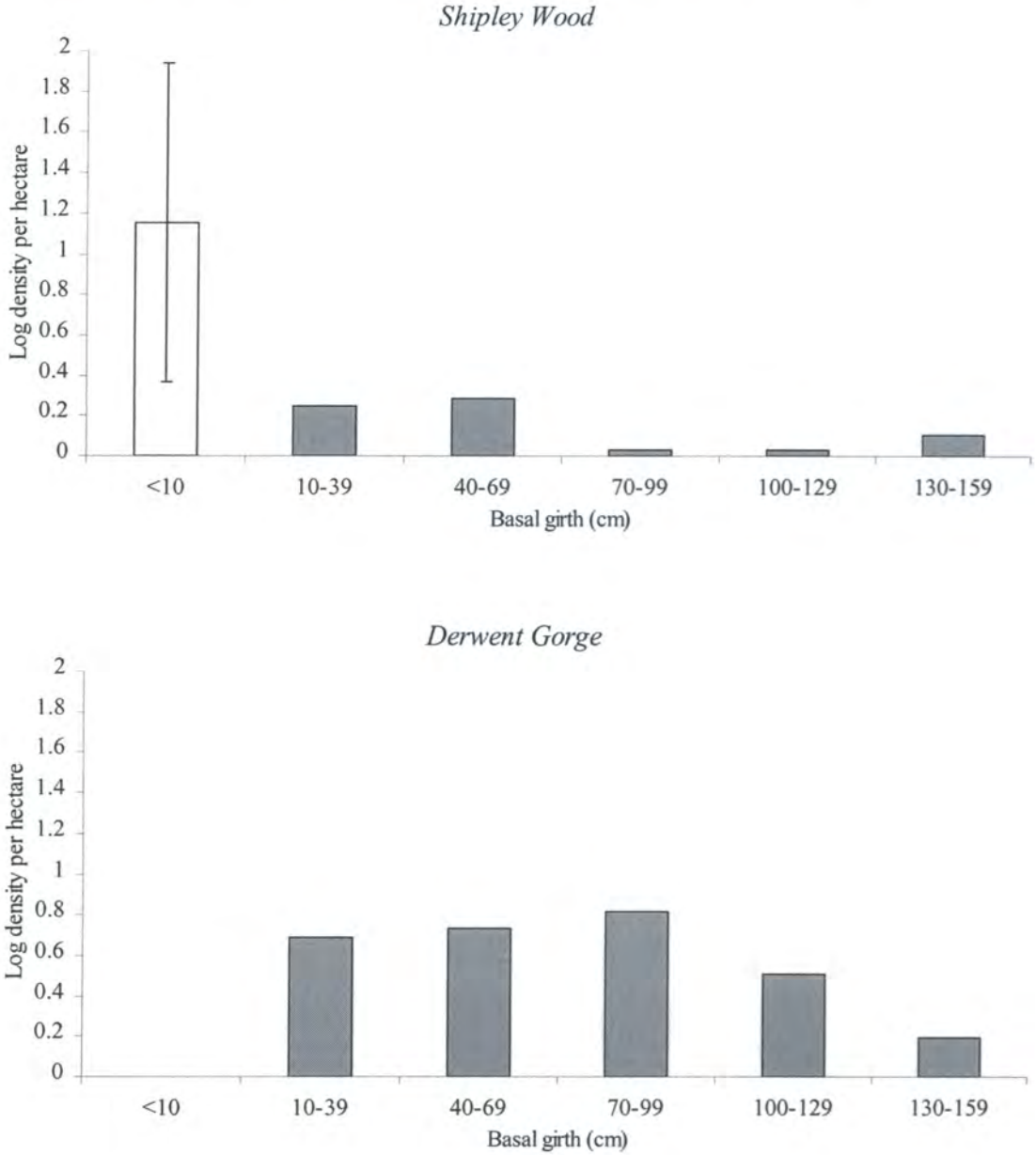


Figure 2.10. The log density (± 1 S.E.) of *Taxus* saplings (basal girth<10cm) and the size distribution of adult tree populations in Shipley Wood and Derwent Gorge.

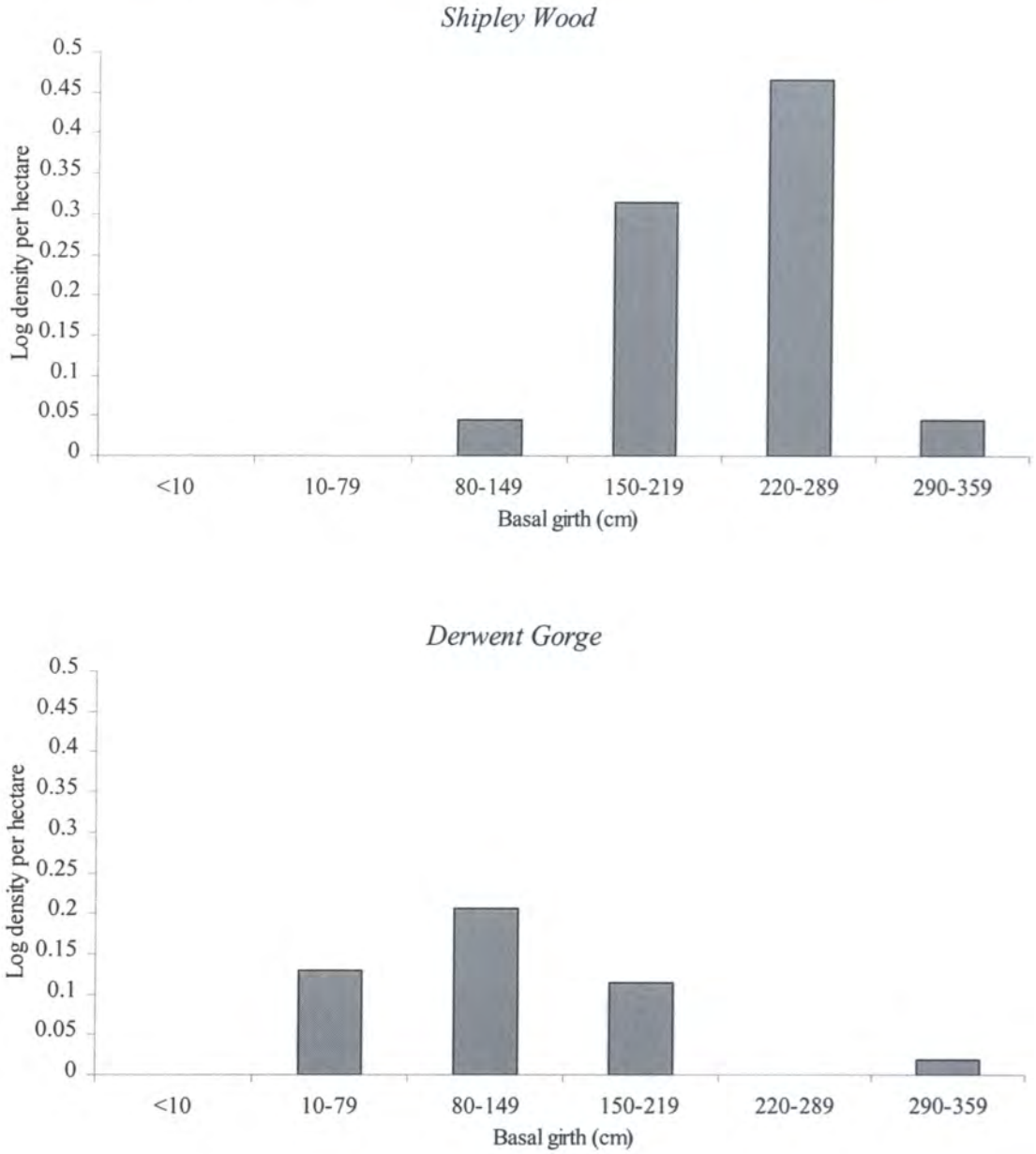
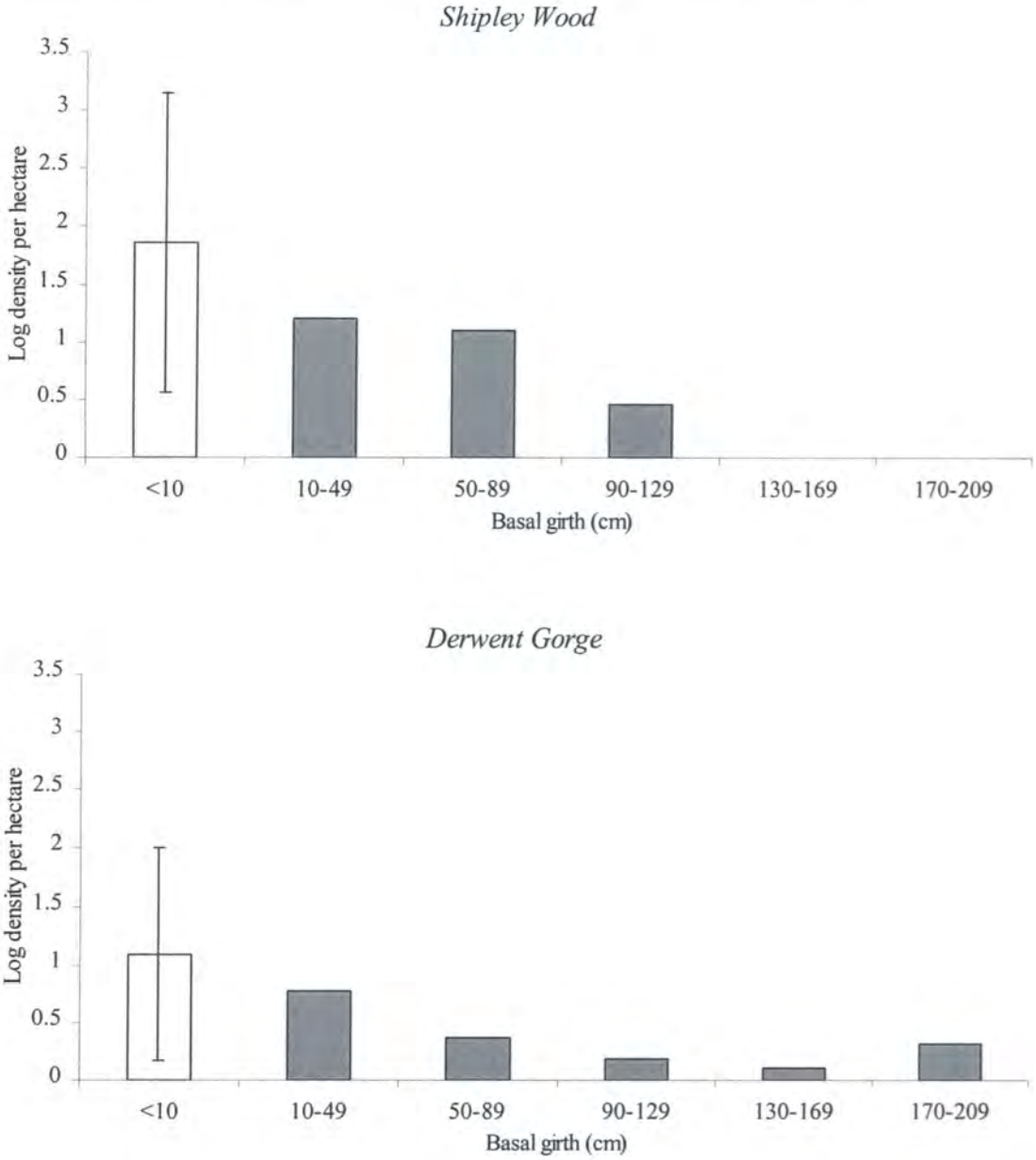


Figure 2.11. The log density (± 1 S.E.) of *Ulmus* saplings (basal girth<10cm) and the size distribution of adult tree populations in Shipley Wood and Derwent Gorge.



2.3.2.4 *Soil pH*

All study species were widely distributed on soils that included the pH ranges measured at Shipley Wood and Derwent Gorge (Table 2.1, Figure 2.4). Soil pH was significantly lower in Derwent Gorge than in Shipley Wood (Table 2.6). Although statistically significant, variation between sites was minimal relative to the wide pH tolerances of the study species and was, therefore, unlikely to have been ecologically significant. Across both sites, soil pH was similar between upper, middle and lower

transects and there was no significant interaction between site and transect (Table 2.6).

Table 2.6. Mean and range of soil pH at upper, middle and lower transects of Shipley Wood and Derwent Gorge. Results of analysis of variance for differences between sites and transects are included. Significance levels (p) were ≥0.05 (n.s., not significant) and <0.05 (✶).

	Shipley Wood		Derwent Gorge	
Transect	Mean	Range	Mean	Range
Upper	5.53	5.23-6.19	4.57	4.09-5.42
Middle	5.61	5.37-6.58	4.61	4.34-6.66
Lower	5.07	4.79-5.6	4.47	3.96-6.09
Total	5.33	4.79-6.58	4.55	3.96-6.66

Source	df	SS	MS	F	p
Site (si)	1	4.3×10^{-9}	4.3×10^{-9}	6.795	✶
Transect (tr)	2	3.5×10^{-10}	1.7×10^{-10}	0.279	n.s.
si x tr	2	1.7×10^{-11}	8.3×10^{-12}	0.013	n.s.
Residual	24	1.5×10^{-8}	6.3×10^{-10}		
Total	29	2.0×10^{-8}	6.8×10^{-10}		

Differences between tree species and study sites in sapling recruitment and adult density, spacing and size distribution most likely reflected contrasting patterns of seed dispersal, survival and germination, and seedling growth, establishment and survival (Clark & Clark, 1984; Morgan, 1987; Goldberg, 1985; Schupp & Fuentes, 1995; Kollmann & Schill, 1996; Oliveira, *et al.*, 1996; Akashi, 1997; Okuda *et al.*, 1997). Differences within and between sites were not accounted for by variation in soil pH. The impact of herbivory on natural regeneration dynamics, relative to alternative biotic and abiotic factors, will be discussed in the chapters that follow.

CHAPTER 3

POST-DISPERSAL SEED PREDATION

3.1 INTRODUCTION

3.1.1 **Studies of post-dispersal seed predation**

For many plant species, the production of seeds and their subsequent dispersal and survival are fundamental components of natural regeneration. Numerous studies, across a wide range of habitats, have investigated the many biotic and abiotic factors limiting plant seed survival. The consumption of nutrient rich seeds by herbivores (seed predators) has often been found to be the most significant source of post-dispersal seed loss (reviewed in Crawley, 1992; Hulme, 1993; Hulme, 1998).

Studies of tree seed predation in temperate deciduous woodland, across a range of countries, are reviewed in Table 3.1. High, variable rates of seed predation were consistently observed. In twenty-two of the twenty-four studies reviewed, including those which directly quantified the relative impact of different predator groups, rodents were found to be the principal agents responsible for seed loss. Ants were the most significant invertebrate group, although in general, invertebrates, birds and larger mammals were of minor importance. While birds do consume seeds, they have a more significant role in frugivory and seed dispersal of fleshy-fruited species (Snow & Snow, 1988). More than half of the studies of seed survival considered only a single plant species, with less than twenty per cent including five or more species.

All studies followed the survival of native woodland tree seeds, whether artificially presented or naturally dispersed. Trials that have presented non-native or commercial seeds may have recorded unnaturally high or low rates of predation, if seeds were especially attractive or avoided as a result of their unfamiliarity (Partridge, 1981). Studies most often incorporated either a seed tray or a cage exclosure. Seed trays could be accessed by all granivores, with seeds presented on the surface of a contained depot. This technique was most effective when the habitat contained only a single category of seed predator or seed loss to other groups had been shown to be negligible. When necessary, seed trays were modified using a lid or a pesticide/adhesive treatment to exclude vertebrates and invertebrates, respectively (treatment modifications represented as 'M' in Table 3.1).

Table 3.1. Review of studies investigating the survival of tree seeds in temperate deciduous woodland. [1] Duration of trial in days unless otherwise stated. Predation rates in parentheses assume unrecovered seeds to have been predated. Open experiment types (O) permit access to all categories of seed predator. Cage exclosures and modified treatments (M) restrict access to specific predator groups. Rates of seed predation varied according to B, seed burial; D, seed density; F, seed frequency; M, microhabitat; P, category of seed predator; S, site; Sp, seed species and T, time of experiment (season/year).

Source	Country	Major predator class	No. of species	Type of experiment	Duration of trial (days)[1]	Rate of seed predation (%)	Source of variation							
							B	D	F	M	P	S	Sp	T
Ashby (1967)	UK	Rodents	3	Seed tray (M)	15	1-100				+			+	+
Boman & Casper (1995)	USA	Rodents	6	Seed tray (O)	21-24	10-100			–	+			+	+
Hulme (1996a)	UK	Rodents	1	Seed tray (O)	3	35-85		–		+		–		
Kollmann *et al.* (1998)	Germany/UK	Rodents	12	Seed tray (O)	50-56	20-100						+	+	+
Tanaka (1995)	Japan	Rodents	3	Seed tray (O)	135	15-100	+						+	+
Webb & Willson (1985)	USA	Rodents	2	Seed tray (O)	1	7-100		–		+		+	+	
Willson & Whelan (1990)	USA	Rodents	10	Seed tray (O)	3	13-29		+		+		+	+	+
Yates *et al.* (1995)	W Australia	Ants	1	Seed tray (M)	1	0-100				+		+		+
Anderson (1987)	SE Australia	Ants	2	Seed plot (M)	10	28-93		+					+	
Sork (1984)	USA	Rodents	1	Seed plot (M)	Autumn-Summer	>99								
Stapanian & Smith (1984)	USA	Rodents	3	Seed plot (O)	27-31			+	+			+	+	+
Wardle (1959)	UK	Rodents	1	Seed plot (M)	31	4-92 (4-98)					+			

Table 3.1. Continued.

Source	Country	Major predator class	No. of species	Type of experiment	Duration of trial (days)[1]	Rate of seed predation (%)	Source of variation							
							B	D	F	M	P	S	Sp	T
Telleria *et al.* (1991)	Spain	Rodents	1	Secured seeds (O)	1	5-90				+		+		
Jensen (1982)	Denmark	Rodents	1	Seed survey	180	1-100		+				+		+
Gardner (1977)	UK	Rodents	1	Cage exclosure	7	0-100				+	+			+
Goldberg (1985)	Mexico	Rodents	1	Cage exclosure	14	52-100						+		
Jensen (1985)	Denmark	Rodents	1	Cage exclosure	45	24-57		+		+				
	Denmark	Rodents	8	Cage exclosure	2-12	25-100							+	
Shaw (1968a)	UK	Rodents (Birds)	1	Cage exclosure	2	98								
(1968b)	UK	Rodents	1	Cage exclosure	11-25	92-100	+				+			+
Wada & Uemura (1994)	Japan	Rodents	1	Cage exclosure	3	32-94 (66-100)				+				
Watt (1919)	UK	Rodents	1	Cage exclosure	11-30	100	+							
Watt (1923)	UK	Rodents	1	Cage exclosure	2-30	4-100	+				+	+		+
Whelan *et al.* (1991)	USA	Rodents	2	Cage exclosure	62/120/150	13-100				+	+		+	+

The most common method of studying seed survival restricts access to the seed supply using cage exclosures, often in combination with a pesticide/adhesive treatment or an elevated seed dish. A combination of all treatments can also be used to quantify levels of background seed loss. This is a particularly effective means of quantifying the relative impact of different animal groups in a habitat containing a mixed suite of seed predators. Animal groups may differ markedly in their relative impact as seed predators and seed dispersers, the quantity of seeds they consume or disperse, the temporal and spatial scales at which they forage and their species and microhabitat preferences. Distinguishing their effects is necessary to assess their relative impacts on plant recruitment.

Alternative techniques include monitoring the survival of seeds (often tagged) broadcast over a larger, defined area (seed plot), or of individual seeds secured to the substrate. The application of pesticide or fencing at the perimeter of a seed plot is an effective means of restricting access to the seed supply. Rather than presenting an experimentally manipulated seed supply, the survival of naturally dispersed seed may also be followed as an effective means of quantifying seed predation. Seed damage is often sufficiently characteristic that the relative importance of different predator groups can be quantified.

Although there was often complete predation of the seed supply, the majority of studies recorded extreme variation in rates of seed loss according to parameters associated with the environment, the food supply and the predator. Spatial variation, between microhabitats and geographically discrete sites, temporal variation (seasonal and annual) and variation between tree species have been most frequently studied.

Variation between microhabitats was found to be significant in all of the studies in which it was investigated, reflecting the foraging activity and microhabitat preferences of the major seed predators (Table 3.1). The spatial heterogeneity of seed loss was most often related to small-scale vegetation structure. In the majority of studies, predator avoidance was a significant constraint on rodent foraging behaviour, with a close spatial association between rates of seed predation, the abundance and activity of rodents and the distribution of protective vegetation cover (Ashby, 1967; Gardner, 1977; Jensen, 1985; Webb & Willson, 1985; Wada & Uemura, 1994; Boman & Casper, 1995; Hulme, 1996a). However, this association was not always consistent among rodent species. For example, the foraging activity of *C. glareolus* is more

closely associated with vegetation cover than that of *A. sylvaticus* (Ashby, 1967; Wada & Uemura, 1994). In addition to the greater structural complexity of regenerating vegetation in gaps, relative to intact forest, Boman and Casper (1995) attributed high seed predation and rodent abundance to the greater seasonal availability of seeds. Webb & Wilson (1985) found that rates of seed predation were greatest directly beneath adult trees, although the relative influence of vegetation cover and seed supply were not distinguished. In contrast, Whelan *et al.* (1991) observed that removal rates were greater in the open forest than at the base of trees and adjacent to logs, and Willson and Whelan (1990) found that preferences for wooded and open field microhabitats were consistently reversed between years. Ashby (1967) also observed that rates of seed loss were greatest from depots in close proximity to rodent burrows.

Differences in predation intensity between geographically discrete sites were found to be significant in nine of the ten studies in which it was investigated (Table 3.1). This spatial heterogeneity was most often attributed to differences in rodent activity (Goldberg, 1985; Webb & Willson, 1985), species (Kollmann *et al.*, 1998) or density (Watt, 1923; Jensen, 1982; Stapanian & Smith, 1984; Goldberg, 1985; Telleria *et al.*, 1991; Kollmann *et al.*, 1998). Consistent with variation between microhabitats, differences in rodent activity were correlated with the availability of protective vegetation cover. Differences in rodent density were related to forest size (Telleria *et al.*, 1991), seed crop size (Watt, 1923) and variation in the cover and composition of forest ground flora (Jensen, 1982; Kollmann *et al.*, 1998). Willson & Whelan (1990) found that the direction of variation between sites differed between years.

Temporal variation in predation intensity was observed in all of the studies in which it was investigated (Table 3.1). Seasonal and annual variation was most often correlated with the natural abundance of conspecific seeds (Watt, 1923; Shaw, 1968b; Gardner, 1977; Jensen, 1982; Stapanian & Smith, 1984; Kollmann *et al.*, 1998) or seeds of other preferred species (Tanaka, 1995), and the population density of rodents (Ashby, 1967; Whelan *et al.*, 1991; Kollmann *et al.*, 1998). With the exception of Kollmann *et al.* (1998), the survival of experimentally supplied seed was enhanced when natural seed availability was high. The seasonal accumulation of leaf litter was also found to reduce rates of seed predation (Boman & Casper, 1995).

All studies investigating more than one plant species found significant variation between species in rates of seed predation (Table 3.1). In general, rodents preferred large, energy rich seeds (Ashby, 1967; Stapanian & Smith, 1984; Jensen, 1985; Willson & Whelan, 1990; Boman & Casper, 1995), although Kollmann *et al.* (1998) found no association between seed size and rates of predation. Other physical and chemical characteristics, including nitrogen content (Jensen, 1985), viability (Kollmann *et al.*, 1998), toxicity (Kollmann *et al.*, 1998), handling time (Stapanian & Smith, 1984), odour content (Stapanian & Smith, 1984) and the percentage of water in the embryo plus endosperm fraction (Kollmann *et al.*, 1998), have also been found to account for rodent seed preferences.

Fewer studies have directly investigated the influence of seed burial, seed density and seed frequency on rates of seed predation in temperate deciduous woodlands. Seed burial was found to be significant in all of the studies in which it was investigated (Table 3.1). Seed survival increased after burial under leaf litter and was further enhanced with increasing depth of burial under soil. Variation with seed density was significant in five of the seven studies in which it was investigated (Table 3.1), although the direction of this response was not consistent. Rates of seed predation were found to either increase with increasing seed density (Stapanian & Smith, 1984; Jensen, 1985), or decrease as a result of predator satiation (Jensen, 1982; Anderson, 1987; Willson & Whelan, 1990). The significance of seed frequency, relative to the availability of alternative food items, also differed between studies. Stapanian & Smith (1984) found that seed survival decreased with the presentation of higher quality food items in mixed grids, whereas Boman & Casper (1995) and Hulme & Hunt (1999) found no effect of seed frequency.

As a result of extreme variation in rates of seed loss, it is difficult to reach general conclusions regarding the impact of seed predation on patterns of plant recruitment. For any particular species, seed survival is likely to depend on the microhabitat to which it is dispersed, the potential for seed burial, the population density and activity of resident seed predators, the density of conspecific seeds and the availability of alternative food items, according to seasonal and annual variation. This may generate quite different patterns of plant recruitment, population dispersion and community composition between similar sites of close proximity. Ultimately,

seed predation may be sufficient to exert selective pressure on seed and plant dispersal characteristics that may reduce the vulnerability of seeds to granivores. Significant impacts on plant demography and evolution are less likely, however, if patterns of seed predation are as variable and unpredictable as previous studies would suggest. For any site of particular scientific and conservation value, it is clearly fundamental to appreciate patterns of post-dispersal seed predation and the potential for spatial and temporal escape, to ensure the regeneration and persistence of species that contribute to their conservation value.

3.1.2 **Study aims**

As part of the broader investigation of herbivory and natural regeneration in temperate deciduous woodland, the principal aim of this study was to quantify the component of post-dispersal seed predation and examine primary sources of variation, the possibility of seed escape and the potential impact on plant population dynamics.

The specific aims, for a range of native tree species, were to;

1. Quantify the relative impact of vertebrate and invertebrate seed predators on the post-dispersal survival of tree seeds in temperate deciduous woodland.
2. Determine whether seed predation varied significantly between plant species and examine the association between rates of removal and seed attributes (physical and chemical).
3. Assess whether seed predation varied spatially, both within and between sites, across a range of microhabitats.
4. Examine whether vertebrate and invertebrate seed predators differ in their species preferences and microhabitat use.
5. Examine the consistency of species and microhabitat preferences between sites, and the consistency of species preferences between microhabitats.

3.2 MATERIALS AND METHODS

3.2.1 **Design of field trials**

Rates of seed loss were quantified using 'cafeteria' trials (Culver & Beattie, 1978) in which food items were presented in feeding depots consisting of a petri-dish (9cm diameter, 1cm depth) buried flush with the ground surface and secured by a central nail. Sampling points comprised three depot types (Table 3.2, Plates 3.1-3.3), using selective exclosure and pesticide treatments to restrict access to specific predator groups: 1) 'Invertebrate' depots incorporated a one centimetre gauge mesh exclosure to permit access to invertebrates only; 2) 'Rodent' depots used a three centimetre gauge mesh exclosure and a molluscicide to permit access to rodents only; 3) 'Open' depots permitted access to all categories of seed predator. Depots were placed at least one metre apart within each sampling point to ensure independence. A mollusc-specific metaldehyde-based pesticide was used at 'Rodent' depots since molluscs were the principal invertebrate seed predators seen feeding at dishes. In laboratory trials, small mammals had no aversion to foraging in the presence of molluscicide or to entering three centimetre mesh exclosures (Hulme 1994a). Molluscicide was replenished at two-week intervals during seed predation trials.

Table 3.2. Depot treatments comprising each sampling point.

Treatment	Exclosure	Molluscicide	Major predators with access
INVERTEBRATE	1cm gauge mesh (14cm x 14cm x 14cm)	None	Invertebrates
RODENT	3cm gauge mesh (13cm diameter x 38cm)	Metaldehyde (Shower-proof Bioslug)	Rodents
OPEN	None	None	All

Seed predation trials were conducted simultaneously at Shipley Wood and Derwent Gorge. Five replicate sampling points were placed in each of nine representative microhabitats, spaced evenly throughout each study site and at least ten metres apart to ensure independence. Sampling points were placed within one metre of the base of adult *Betula*, *Fraxinus*, *Ilex*, *Sorbus*, *Taxus* and *Ulmus*, beneath coppiced adults of *Corylus avellana* (Shrub) and beneath the dense cover of *Pteridium aquilinum* (High Vegetation). Replicates were placed beneath adult trees of a similar

Plates 3.1-3.3. Depot treatments comprising each sampling point.

Plate 3.1 'Invertebrate' depot

>1m

>1m

Plate 3.2 'Rodent' depot

>1m

Plate 3.3 'Open' depot

size. Open microhabitats were also sampled, typically consisting of a mixture of low lying grasses, herbs, moss and litter, providing minimal cover of less than five centimetres in height.

Seed predation trials were conducted for each of the study species, which differed in seed size, fruiting time, dispersal mechanism and adult density (Table 3.3). Seeds presented during trials were collected from adults of each study species at the time of fruit maturation and seed dispersal. Samaras of *Fraxinus* and *Ulmus* were collected directly from fruiting adults. Strobiles of *Betula* were stripped and shattered to separate the samara from bracts. Arillate seeds of *Taxus* and berries of *Ilex* and *Sorbus* were collected and macerated with water to extract seeds. Seeds of all species were sorted to discard those which were damaged or infertile, and kept in dry storage at room temperature.

Table 3.3. Fruiting characteristics of each study species. Seed masses (mg dry weight per seed) were exclusive of dispersal structures. Dispersal periods and agents were taken from [1] Gardner (1977), [2] Grime *et al.* (1988) and [3] Snow & Snow (1988). Adult densities (trees per hectare) in Shipley Wood and Derwent Gorge were estimated using the point-centred quarter method (Chapter 2).

Taxon	Dispersal period	Dispersal agent	Seed mass (mg dwt seed^{-1})	Adult density (trees ha^{-1})	
				Shipley Wood	Derwent Gorge
Fraxinus	Spring [1]	Wind [2]	51.70	91.6	49.1
Ulmus	Spring [2]	Wind [2]	9.80	28.7	8.1
Sorbus	Summer [3]	Birds [3]	3.80	2.1	16.6
Taxus	Summer [3]	Birds [2]	48.20	3.2	1.3
Betula	Autumn [2]	Wind [2]	0.20	88.6	10.0
Ilex	Autumn [3]	Birds [3]	20.35	2.2	2.2

Seed predation trials commenced on November 26th, 1995 and were terminated on March 28th, 1996. Ten seeds of each species were presented at each sampling point in a unique randomised order. Depots within each sampling point received the same species of seed during each trial. Trials extended for three days to allow the resources to be fully exploited. At the end of each trial, the number of seeds remaining intact was recorded, giving a measure of seed predation. Seed removal was assumed to result in seed death, through either consumption away from the depot or dispersal to unfavourable germination microsites. Seed remains were then cleared from each depot and the seed supply replenished. Trials continued until every sampling point had received seed of each species.

3.2.2 **Analysis of seed characteristics**

Selected physical and chemical characteristics of each species were measured. Dispersal structures (wings or fleshy pulp) were removed from forty seeds of each species. Seeds were dried in a vacuum oven for forty-eight hours at forty degrees centigrade and the dry masses of whole seeds and their endosperm/embryo component measured. Testa mass and the ratio of testa mass to total mass were also calculated for each species. For seeds of *Betula*, *Fraxinus*, *Taxus* and *Ulmus*, energy values for the endosperm plus embryo fraction were taken from Jensen (1985) and Smal & Fairley (1980). Equivalent energy values for *Ilex* and *Sorbus* were determined using a Gallenkamp ballistic bomb-calorimeter (Grodzinski & Sawicka-Kapusta, 1970). Samples were prepared in the form of a pellet, with a dry weight of 0.3-0.4g. Calorific determinations were made using five samples of each species, from which mean energy values were calculated.

A colorimetric test was used to determine the viability of ten seeds collected from each of ten fruiting adults of each species. Seeds were sectioned and incubated at fifty degrees centigrade in a solution of 0.5% tetrazolium blue chloride for two to four hours. Metabolising cells were identified by a positive pink colour change, from which seed viability was determined.

3.2.3 **Statistical analysis**

Seed predation data were analysed according to Hulme (1994a), distinguishing seed 'encounter', the probability of at least one seed being predated from a depot (binary variable; encountered or not encountered), from seed 'exploitation', the proportion of seeds predated once encountered. Distinction could not be made between seeds never located by seed predators and seeds located, but subsequently ignored, although both were equivalent from the plant's perspective since neither influenced seed mortality (Hulme & Hunt, 1999). The experimental design combined both fixed effect (microhabitat, treatment and species) and random effect (site) factors (Zar, 1984). As such, seed encounter and exploitation were most appropriately analysed using a 'mixed model' or 'Model III' factorial analysis of variance in GLIM, assuming a binomial error distribution (NAG, 1985).

The spatial associations between rates of seed encounter and exploitation at Rodent and Open depots were investigated. Bivariate categorical data for seed encounter were analysed using a two-way frequency table, with a Yates corrected

Chi-squared statistic for continuity. The association for bivariate numerical seed exploitation data was determined using the Pearson sample correlation coefficient, for the arcsine transformed proportion of seeds exploited.

For each treatment, Pearson sample correlations were used to examine the association between seed characteristics (total seed dry mass, endosperm plus embryo dry mass, testa dry mass, testa mass:total mass ratio, energy content and seed viability) and the arcsine transformed proportion of seeds encountered and exploited.

3.3 RESULTS

3.3.1 **Seed Encounter**

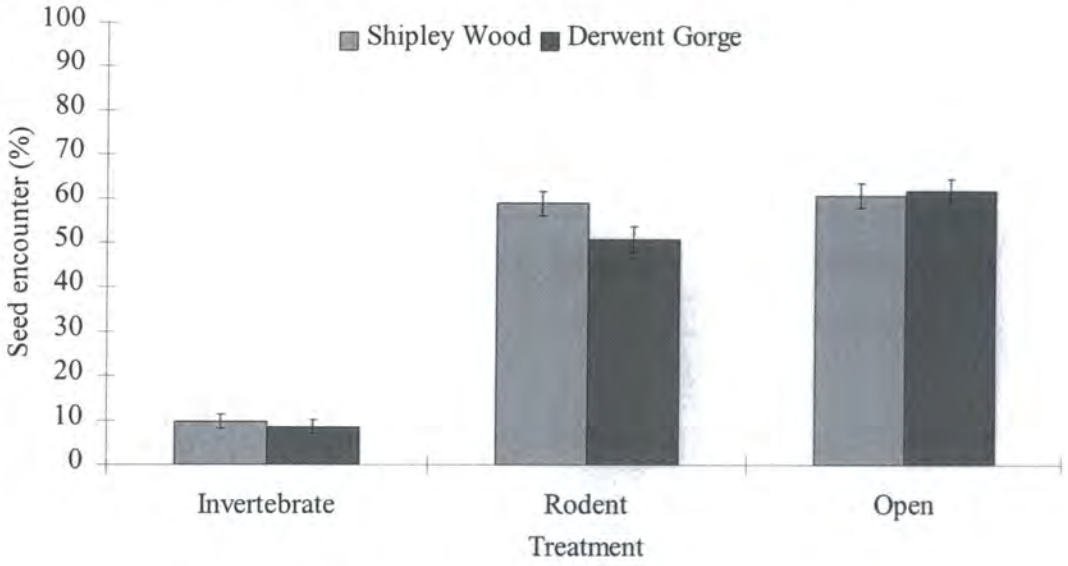
3.3.1.1 *Variation between treatments*

Rates of seed encounter varied significantly between treatments, and variation between treatments was similar between sites (Table 3.4, Figure 3.1). Seed encounter was low at Invertebrate depots (<10%) relative to the other treatments. At Rodent and Open depots, rates of encounter were of a similar magnitude (t_{1078}=1.661, p>0.05) and were highly spatially associated (χ^2_1=145.998, p<0.001).

Table 3.4. Total variation in seed encounter (across all treatments) partitioned between the main effects (site, microhabitat, species and treatment) and their higher order interactions. Significance levels (p) were ≥0.05 (n.s., not significant), <0.05 (✶), <0.01 (✶✶) and <0.001 (✶✶✶).

Source	df	SS	MS	F	p
Site (si)	1	1.23	1.23	1.43	n.s.
Microhabitat (mh)	8	37.90	4.74	1.08	n.s.
Species (sp)	5	184.50	36.90	15.64	✶✶
Treatment (tr)	2	467.80	233.90	137.59	✶
si.mh	8	34.94	4.37	5.07	✶✶✶
si.sp	5	11.81	2.36	2.74	✶
si.tr	2	3.39	1.70	1.97	n.s.
mh.sp	40	64.62	1.62	1.31	n.s.
mh.tr	16	48.21	3.01	3.46	✶
sp.tr	10	27.25	2.73	1.73	n.s.
si.mh.sp	40	49.44	1.24	1.44	n.s.
si.mh.tr	16	13.90	0.87	1.01	n.s.
si.sp.tr	10	15.80	1.58	1.83	n.s.
mh.sp.tr	80	96.98	1.21	3.56	✶✶✶
si.mh.sp.tr	80	26.90	0.34	0.39	n.s.
Residual	1294	1114.4	0.8612		
Total	1617	2199.1			

Figure 3.1. Mean percentage seed encounter (± 1 S.E.) for each treatment, at both sites.



3.3.1.2 *Spatial variation*

Patterns of microhabitat use varied significantly between sites (Table 3.4, Figure 3.2). The majority of microhabitats were of similar importance in both sites, with seed encounter lowest in open microhabitats. Sites differed principally in the use of *Fraxinus* and High Vegetation microhabitats (t_{178}=2.798, p<0.01 and t_{178}=3.547, p<0.001, respectively). Seed encounter beneath adults of *Fraxinus* was proportionally greater in Shipley Wood, whereas, encounter beneath High Vegetation was proportionally greater in Derwent Gorge.

Contrasting microhabitat use by different predator groups was evident from the interaction between treatment and microhabitat (Table 3.4, Figure 3.3), with similar patterns found in both sites. At Open depots, seed encounter was greatest beneath adults of *Ilex* and decreased progressively from Shrub to High Vegetation and Open microhabitats. Rates of encounter were similar at Rodent depots, differing principally in the use of *Ilex* and *Taxus* microhabitats (t_{118}=2.517, p<0.05 and t_{118}=3.100, p<0.01, respectively). Across all microhabitats, rates of seed encounter at Rodent and Open depots were highly spatially associated (χ^2_1=145.998, p<0.001). Invertebrate encounter was low across all microhabitats, and was only greater than fifteen percent beneath High vegetation. Consistent with Rodent and Open treatments, invertebrate encounter was lowest in the open. At both sites, variation between treatments in patterns of microhabitat use was species dependent (Table 3.4).

Figure 3.2. Mean percentage seed encounter (± 1 S.E.) for each site, across all microhabitats (*Betula* [Bp], *Fraxinus* [Fe], *Ilex* [Ia], *Sorbus* [Sa], *Taxus* [Tb], *Ulmus* [Ug], Shrub [SH], High vegetation [HV] and Open [OP]).

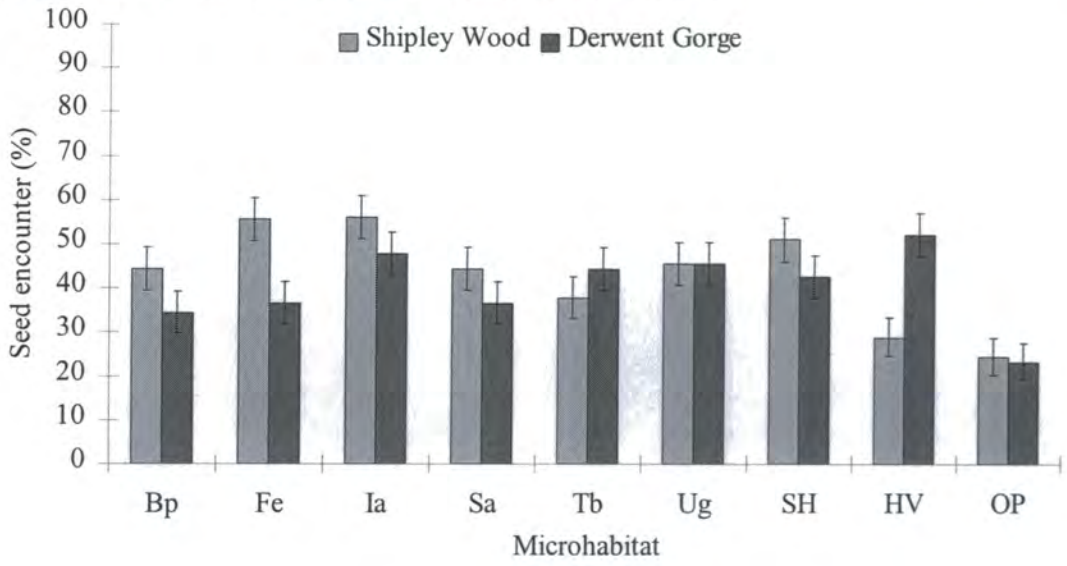
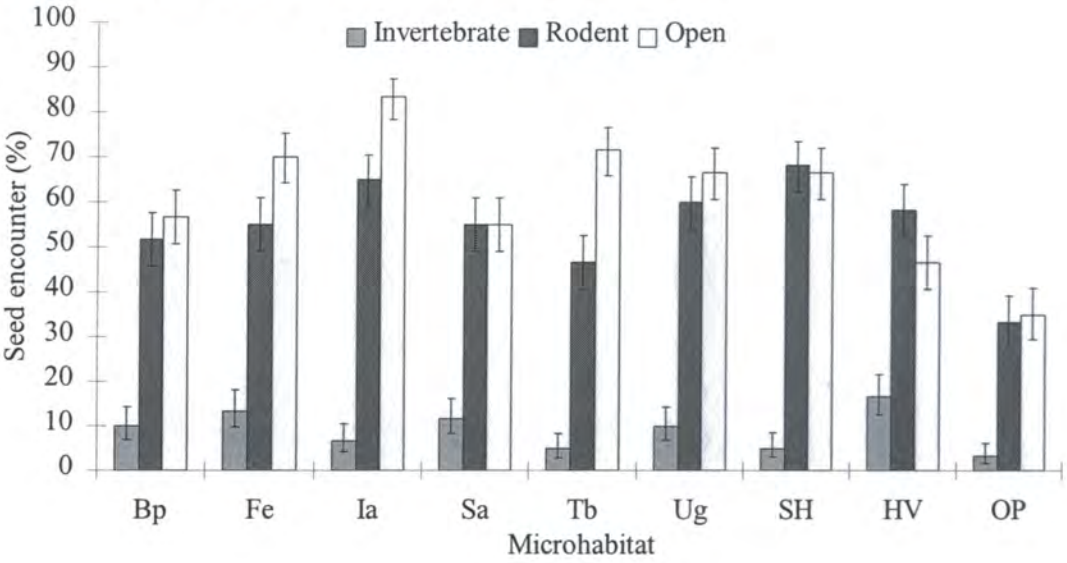


Figure 3.3. Mean percentage seed encounter (± 1 S.E.) for each treatment, across all microhabitats (*Betula* [Bp], *Fraxinus* [Fe], *Ilex* [Ia], *Sorbus* [Sa], *Taxus* [Tb], *Ulmus* [Ug], Shrub [SH], High vegetation [HV] and Open [OP]).

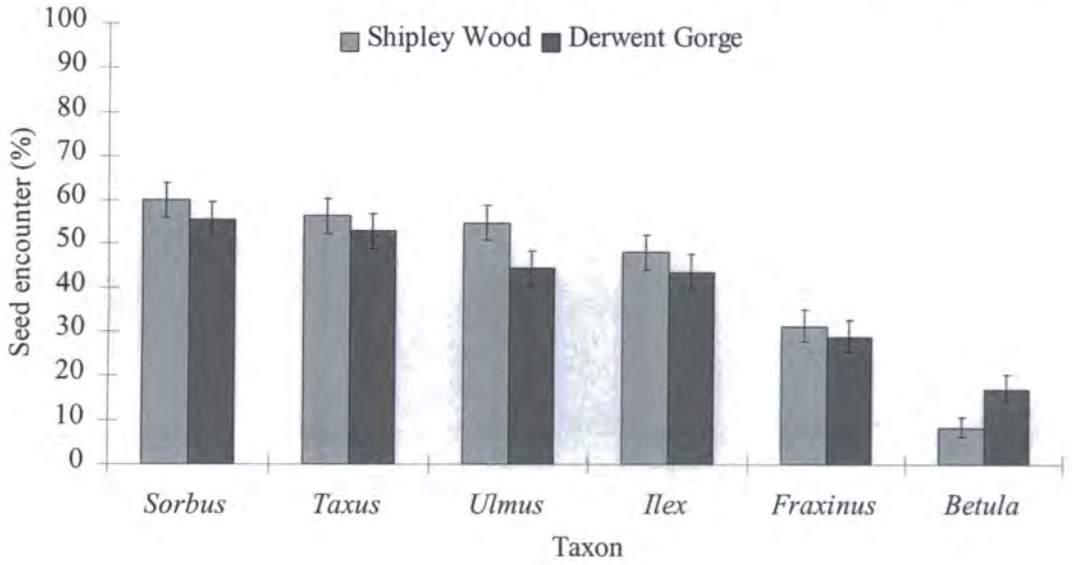


3.3.1.3 *Variation between species*

Rates of encounter varied significantly between species (Table 3.4), ranging from 13% to 58%. In both sites, taxa were ranked in the same order of preference, although rates of *Betula* seed encounter were proportionally greater in Derwent Gorge than in Shipley Wood (t_{268}=2.401, p<0.05, Table 3.4, Figure 3.4). Seeds of *Taxus* and *Sorbus* were most frequently encountered, and seeds of *Fraxinus* and *Betula* least

encountered. At both sites, variation across species was similar between treatments and between microhabitats (Table 3.4). There was no evidence to support the preferential encounter of conspecific seeds beneath adult trees, and there was no combined interaction between site, microhabitat, species and treatment (Table 3.4).

Figure 3.4. Mean percentage seed encounter (± 1 S.E.) for each species, at both sites.



3.3.2 **Seed exploitation**

As a result of variation in the proportion of seeds encountered, the available data for seed exploitation was highly heterogenous. The resulting constraints between factors compromised their independence such that the data could not be analysed in their entirety using GLIM. To minimise this heterogeneity, it was necessary to exclude those variables for which seed exploitation data were sparse, with encounter rates averaging less than twenty percent. The exploitation of *Betula* seeds and all removal from Invertebrate depots was, therefore, omitted for more reliable analysis of the remaining variables.

3.3.2.1 *Variation between treatments*

Rates of seed exploitation did not vary significantly between Rodent and Open depots (83.8 and 79.6%, respectively), nor between Shipley Wood and Derwent Gorge (82.5 and 80.6%, respectively), and there was no significant interaction between site and treatment (Table 3.5). Rates of encounter at Rodent and Open depots were also highly spatially correlated (r_{243}=0.544, p<0.001).

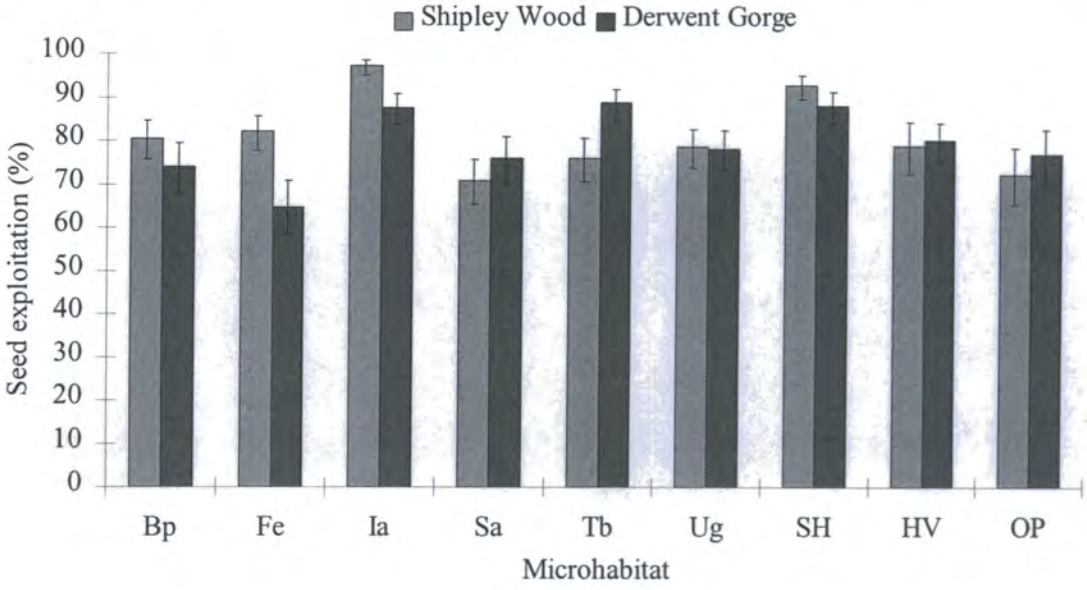
Table 3.5. Total variation in seed exploitation (across Rodent and Open treatments, excluding *Betula*) partitioned between the main effects (site, microhabitat, species and treatment) and their higher order interactions. Probabilities were ≥0.05 (n.s., not significant), <0.05 (✶), <0.01 (✶✶) and <0.001 (✶✶✶).

Source	df	SS	MS	F	*p*
Site (si)	1	3.62	3.62	0.81	n.s.
Microhabitat (mh)	8	205.20	25.65	1.78	n.s.
Species (sp)	4	723.50	180.88	46.03	✶✶
Treatment (tr)	1	3.75	3.75	11.36	n.s.
si.mh	8	115.40	14.43	3.21	✶✶
si.sp	4	15.70	3.93	0.87	n.s.
si.tr	1	0.33	0.33	0.07	n.s.
mh.sp	32	250.70	7.83	1.79	n.s.
mh.tr	8	25.28	3.16	0.43	n.s.
sp.tr	4	37.24	9.31	2.61	n.s.
si.mh.sp	32	139.90	4.37	0.97	n.s.
si.mh.tr	8	58.38	7.30	1.62	n.s.
si.sp.tr	4	14.29	3.57	0.79	n.s.
mh.sp.tr	31	179.20	5.78	2.32	✶
si.mh.sp.tr	28	69.61	2.49	0.55	n.s.
Residual	424	1908.00	4.50		
Total	598	3749.90			

3.3.2.2 *Spatial variation*

Patterns of microhabitat use varied significantly between sites (Table 3.5, Figure 3.5). The sites differed principally in the use of *Fraxinus* (t_{65}=2.308, p<0.05), *Ilex* (t_{83}=2.408, p<0.05) and *Taxus* (t_{68}=2.114, p<0.05) microhabitats. Seed exploitation beneath adults of *Ilex* and *Fraxinus* was proportionally greater in Shipley Wood, whereas, exploitation beneath *Taxus* was proportionally greater in Derwent Gorge. Treatments did not differ significantly in patterns of microhabitat use, in either site, although variation was species dependent (Table 3.5).

Figure 3.5. Mean percentage seed exploitation (± 1 S.E.) for each site, across all microhabitats (*Betula* [Bp], *Fraxinus* [Fe], *Ilex* [Ia], *Sorbus* [Sa], *Taxus* [Tb], *Ulmus* [Ug], Shrub [SH], High vegetation [HV] and Open [OP]).

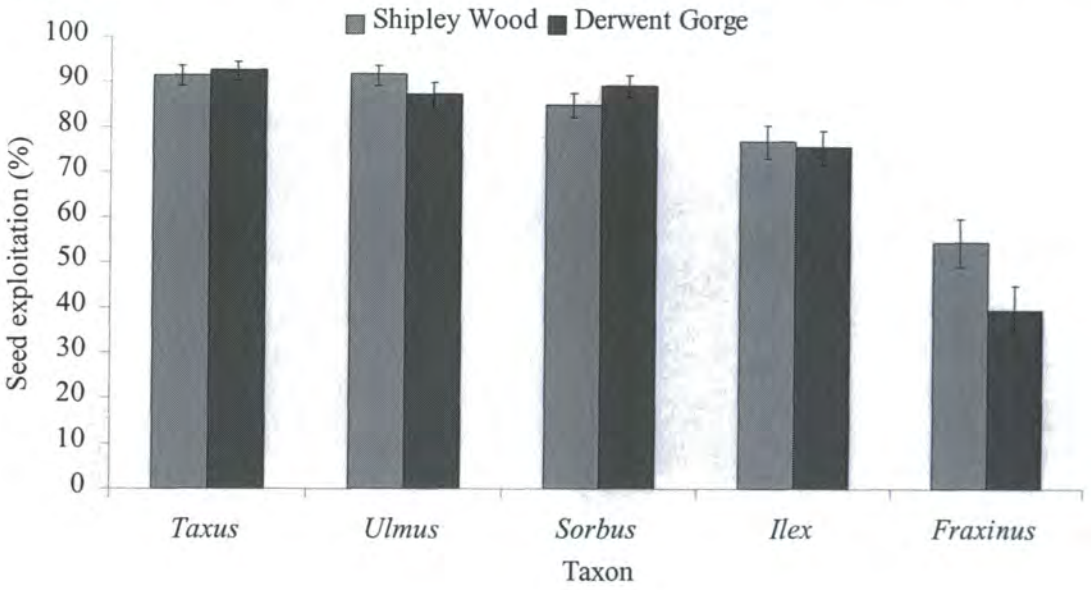


3.3.2.3 *Variation between species*

Rates of exploitation differed significantly between species (Figure 3.6), and variation between species was similar between sites, microhabitats and treatments (Table 3.5). With the exception of *Fraxinus*, once encountered the majority of seeds of each taxon were exploited (>75%). There was no evidence to support the preferential exploitation of conspecific seeds beneath adult trees, and there was no interaction between site, microhabitat, species and treatment (Table 3.5).

Across all species for which both seed encounter and seed exploitation data were available, rates of encounter were correlated with rates of exploitation at rodent and open depots ($r=0.912$, $df=3$, $p<0.05$ and $r=0.896$, $df=3$, $p<0.05$, respectively). Species which were most frequently encountered were also most frequently exploited.

Figure 3.6. Mean percentage seed exploitation (± 1 S.E.) for each species, at both sites.



3.3.3 **Variation with respect to seed characteristics**

Rates of seed encounter and exploitation at Invertebrate, Rodent and Open depots were not significantly associated with any of the physical or nutritional parameters measured (Tables 3.6 and 3.7). Total seed mass, endosperm plus embryo mass, testa mass, testa mass:total mass ratio, energy content and seed viability were, therefore, poor predictors of seed encounter and exploitation.

Table 3.6. Characteristics of tree seeds for each study species. All seeds were analysed without dispersal structures. Energy values taken from [1]Jensen (1985) and [2]Smal & Fairley (1980) or [3]measured using bomb calorimetry, are shown in calories per mg dry weight (cal/mg dwt) and calories per seed (cal/seed). Mass values are shown in mg dry weight per seed (mg dwt/seed).

Taxon	Total mass	Endosperm plus embryo mass	Testa mass	Testa mass/ Total mass	Energy content of endosperm plus embryo		Seed viability
	mg dwt/seed	mg dwt/seed	mg dwt/seed		cal/mg dwt	cal/seed	(%)
Betula	0.20	0.05	0.15	0.75	[1] 6.06	0.30	13
Fraxinus	51.70	34.75	16.95	0.33	[1] 6.28	218.23	89
Ilex	20.35	5.85	14.50	0.71	[3] 7.73	45.22	58
Sorbus	3.80	1.80	2.00	0.53	[3] 6.46	11.63	94
Taxus	48.20	21.25	26.95	0.56	[2] 8.41	178.71	100
Ulmus	9.80	8.85	0.95	0.10	[1] 6.40	56.64	38

Table 3.7. Results of Pearson sample correlations between seed characteristics and the proportion of seeds encountered and exploited. Pearson (r) correlation coefficients and degrees of freedom (df) are included for each treatment. Significance levels (p) were ≥0.05 (n.s., not significant).

	Invertebrate			Rodent			Open		
Encounter	r	df	*p*	r	df	*p*	r	df	*p*
Endosperm plus embryo mass	-0.670	4	n.s.	-0.022	4	n.s.	0.174	4	n.s.
Testa mass	-0.457	4	n.s.	-0.099	4	n.s.	0.155	4	n.s.
Total mass	-0.622	4	n.s.	-0.062	4	n.s.	0.180	4	n.s.
Testa /Total mass	0.710	4	n.s.	0.612	4	n.s.	0.635	4	n.s.
Energy/mg dwt	-0.241	4	n.s.	-0.356	4	n.s.	-0.170	4	n.s.
Energy/seed	-0.685	4	n.s.	-0.106	4	n.s.	0.119	4	n.s.
Seed viability	-0.731	4	n.s.	-0.130	4	n.s.	0.041	4	n.s.
Exploitation	r	df	*p*	r	df	*p*	r	df	*p*
Endosperm plus embryo mass	—	—	—	-0.422	3	n.s.	-0.737	3	n.s.
Testa mass	—	—	—	0.056	3	n.s.	-0.309	3	n.s.
Total mass	—	—	—	-0.231	3	n.s.	-0.604	3	n.s.
Testa /Total mass	—	—	—	0.036	3	n.s.	0.022	3	n.s.
Energy/mg dwt	—	—	—	0.531	3	n.s.	0.302	3	n.s.
Energy/seed	—	—	—	-0.252	3	n.s.	-0.616	3	n.s.
Seed viability	—	—	—	0.228	3	n.s.	-0.021	3	n.s.

3.3.4 **Impact of predator groups**

In addition to the use of exclosure techniques, the consumption of seeds by rodents and invertebrates '*in situ*' was easily distinguished from seed remains. The presence of faeces and mucus was also characteristic of each group. Molluscs (including *Arion* spp. and *Agriolimax* spp.) were the only invertebrates and rodents (including *Clethrionomys glareolus*) the only mammals seen feeding at dishes. Birds were frequently seen consuming fruit of *Ilex*, *Taxus* and *Sorbus* from fruiting adults, but were not observed foraging on seeds at dishes on the woodland floor.

3.4 DISCUSSION

3.4.1 **Impact of predator groups**

Rates of encounter and exploitation were not significantly different between Rodent depots and those open to all categories of seed predator (Figure 3.1, Table 3.5). Patterns of species variation and microhabitat use were also similar between Rodent and Open depots (Figure 3.3, Table 3.5), where rates of seed loss were highly spatially correlated. In addition, the relative proportion of exploited seeds consumed *in situ* and removed from depots were similar between Rodent (40.6 and 59.4%, respectively) and Open (36.9 and 66.1%, respectively) treatments. Rodents were, therefore, likely to be the principal agents responsible for seed encounter and exploitation. This was confirmed by the presence of rodent faeces and characteristic seed remains at open depots, and was consistent with other studies of tree seed survival in temperate deciduous woodland (Table 3.1). Background seed loss and that attributable to invertebrates and other categories of seed predator was of minor importance.

3.4.2 **Rodent foraging behaviour**

In order to interpret patterns of species and microhabitat variation, it is necessary to appreciate the behavioural, morphological and physiological mechanisms involved in rodent foraging. According to Hulme (1993), rodent seed predation can be considered as a number of sequential steps. Appetitive behaviour, driven by hunger, involves the detection, identification, procurement and handling of the food item, which culminates in consumption.

It has been well documented that rodents primarily use olfactory, rather than visual, cues in detecting and identifying seed as food (Howard *et al.*, 1968; Lockard & Lockard, 1971; Jennings, 1976). The probability of seeds being encountered depends on a number of factors, principally the olfactory acuity (Price, 1978) and foraging efficiency (Collier & Collier, 1981; Armstrong *et al.*, 1987; Baum, 1987) of the rodent, as well as the olfactory conspicuousness of the seed (Reichman, 1981). This is thought to be generated by the emission of volatile chemicals from the seed, where the odour concentration provides cues as to the identity, location and density of the seed supply. Seed burial, seed size, seed density and testa thickness may all influence odour concentration and the detection of seeds, although in the present study seed size and testa thickness were not associated with rates of encounter.

Once encountered, the decision to exploit the resource depends on the perceived quality of the food item (nutritional value, toxicity) from olfactory cues, its familiarity and the availability of alternative foods. The cost of procuring seeds is negligible when on the soil surface, generally increasing with depth of burial according to the substrate type (soil particle size, compactness and water content) and the excavation efficiency of the forager. Acquired seed may then be harvested (husked and consumed), stored in a cache for later consumption, or rejected and searching continued. The probability that a seed is harvested once encountered depends on its suitability as a food source, the ease with which it can be harvested and the availability of alternative foods.

In general, foraging is governed by various 'decision rules' which attempt to minimise the constraints on an animal's performance (e.g. energy expenditure) and maximise its benefits (e.g. dietary intake). 'Optimal foraging theory' states that given a range of food items, the forager will select those which optimise the goal being pursued (Emlen & Emlen, 1975; Pulliam, 1975a,b; Collier & Collier, 1981; Ollason, 1987). The maximisation of energy intake is a common goal (Pulliam, 1975a; Reichman, 1977; Kelrick *et al.*, 1986; Frank, 1988; Kerley & Erasmus, 1991), which has been investigated with respect to seed size (Ashby, 1967; Boman & Casper, 1995; Henderson, 1990; Jensen, 1985; Price, 1983; Stapanian & Smith, 1984; Willson & Whelan, 1990), seed density (Greenwood, 1985; Jensen, 1985; Lacher *et al.*, 1982; Stapanian & Smith, 1984) and lipid content (Smith & Follmer, 1972; Hansson, 1973; Price, 1983; Kerley & Erasmus, 1991).

Plants possess a number of traits that afford some degree of protection against predators, including the synthesis of toxic, anti-nutritional secondary metabolites. The presence of these compounds, which include enzyme inhibitors, haemagglutinins and cyanogenic glucosides, is likely to be an important seed characteristic influencing rodent selectivity (Janzen, 1971; Kollmann *et al.*, 1998). The physical characteristics of a seed, such as seed size or thickness of the seed coat, may impose handling time constraints which influence rates of predation (Stapanian & Smith, 1984). A thick and impermeable testa may also reduce the emission of volatile chemicals, thus reducing their olfactory conspicuousness and detection (Stapanian & Smith, 1984). Seed size influences handling time in a relationship which is likely to be U-shaped, with an optimum range of seed sizes for a particular species of rodent. Handling times would

increase for seeds larger and smaller than this range. The nitrogen content (Jensen, 1985) and viability (Kollmann *et al.*, 1998) of seeds, and the percentage of water in the embryo plus endosperm fraction (Kollmann *et al.*, 1998), have also been found to account for rodent seed preferences.

3.4.3 **Variation between species**

In the present study, rates of seed encounter and exploitation varied significantly between species (Tables 3.4 and 3.5, Figures 3.4 and 3.6), indicating that seed predators were making selective, rather than random, foraging decisions. Since rodents were the principal agents responsible for seed encounter and exploitation, the overall rank order of species reflected rodent seed 'preferences'. This ranking was the same in both sites, demonstrating the consistency with which rodents select food items, and was similar between encounter and exploitation. Species which were most frequently encountered were also most frequently exploited.

Rodent encounter and exploitation were greatest for seeds of *Sorbus*, *Taxus* and *Ulmus*, with seeds of *Ilex* slightly less exploited, and least for seeds of *Fraxinus* and *Betula*. Smal & Fairley (1980) found broad support for these seed preferences in a laboratory study investigating the food of *Apodemus sylvaticus* (wood mouse) and *Clethrionomys glareolus* (bank vole), although they also found differences between rodent species. Seeds of *Taxus* were highly preferred by both *A. sylvaticus* and *C. glareolus*, which principally consumed endosperm. Ripe seeds of *Ilex* were readily consumed by *A. sylvaticus*, but were less palatable to *C. glareolus*. When an alternative food supply (coconut) was available, *C. glareolus* did not select *Ilex* seeds. Seeds of *Fraxinus* were largely rejected by *A. sylvaticus*, particularly when an alternative food supply was available, whereas *C. glareolus* consumed them readily. Seeds of *Sorbus* were also found to be readily consumed by *C. glareolus* during feeding trials (Drozdz, 1966).

The rejection of *Fraxinus* seeds by *A. sylvaticus* was supported in the field by Ashby (1967), whereas other studies found a mixed reaction by *C. glareolus* to seeds of *Fraxinus*, which were either preferred (Flowerdew & Gardner, 1978, field) or rejected (Ashby, 1967, field; Zemanek, 1972, laboratory). Wardle (1959) also recorded high rates of *Fraxinus* seed predation by rodents, whereas Watts (1968) found that *Fraxinus* seeds were only eaten sparingly at a time when the availability of alternative seed was low (spring/early summer). In the present study, intermediate

rates of *Fraxinus* seed encounter and exploitation at Rodent depots (31.1 and 57.5 %, respectively), rather than preference or complete rejection, may reflect either the combined, mixed reaction of different rodent species or the low natural availability of alternative seed.

Seed preferences were not correlated with any of the physical (total seed mass, endosperm plus embryo mass, testa mass, testa mass:total mass ratio or seed viability) or nutritional (energy content per gram or per seed) parameters measured (Table 3.6 and 3.7). Studies investigating tree seed survival in temperate deciduous woodland (Table 3.1) most often found that rodents preferred large, energy rich seeds (Ashby, 1967; Boman & Casper, 1995; Jensen, 1985; Stapanian & Smith, 1984; Willson & Whelan, 1990), with similar preferences observed in laboratory trials (Grodzinsky & Sawicka-Kapusta, 1970; Jensen, 1985). Kollmann *et al.* (1998), however, found no association between seed size and rates of predation, consistent with the present study, and found that predation rates were lowest for toxic species and species with woody endocarps.

It is likely that toxicity was a significant factor in the consumption of *Fraxinus* seeds, which had a high endosperm mass and energy content, and a relatively thin testa (Table 3.6), yet were of low preference to rodents. The mixed reaction to *Ilex* may also reflect some degree of toxicity. Smal & Fairley (1980) found that *Taxus* had a calorific value that exceeded that of any other plant taxon recorded at the time of their investigation. Preference for this species would suggest that such a high energy content was not significantly outweighed by an intolerable degree of toxicity. In laboratory feeding trials, *A. sylvaticus* and *C. glareolus* survived on an exclusive diet of *Taxus* seeds (Smal & Fairley, 1980). In contrast, individuals of *A. sylvaticus* died on an exclusive diet of *Fraxinus* and unripe *Ilex* seeds after only three and two days, respectively, and individuals of *C. glareolus* died on an exclusive diet of ripe and unripe *Ilex* seeds after only two days. Such acute mortality would support differences in toxicity.

Although there was no overall association between seed mass and rates of encounter, seeds of *Betula* may have remained largely undiscovered as a result their small size (0.20mg dwt seed^{-1}), relative to alternative taxa. In addition, the time and energy necessary to manipulate and consume such small seeds may have been considerably greater relative to the energy gains available. Jensen (1985) found that of ten deciduous tree taxa, seeds of *Betula* were the smallest and had the lowest removal

rates in the field (<25% after 12 days). In fact, rodents were found to show 'little interest in seeds of *Betula*', with the disappearance of seeds mainly attributed to accidental loss and digging. Laboratory trials also supported low preference ratings for taxa with small seeds, including *Betula*. Although large seeds tend to be predated more than small seeds (Jensen, 1985; Willson & Whelan, 1990), seed size is rarely the exclusive factor accounting for variation in seed loss (Jennings, 1976). In grassland, Hulme (1994a) recorded similar, high rates of encounter and exploitation for small (<1mg; 60.00% and 76.01%, respectively) and large (>1mg; 50.91% and 71.43%, respectively) surface seeds at high density (10 seeds).

Although there was no overall association between seed viability and rates of seed encounter and exploitation in the present study, the very low viability of *Betula* seeds (13%) most likely contributed to the infrequent encounter of this taxon, particularly if rodents possessed the olfactory acuity to make such distinctions prior to seed acquisition.

It is clearly difficult to draw general conclusions regarding the parameters that determine seed preferences in temperate deciduous woodlands. For the majority of species, it is likely that seed preferences are individualistic responses, ultimately governed by trade-offs between handling time, nutritional content ('nutrient hypothesis') according to dietary requirements, the avoidance of noxious plant chemical defences ('secondary chemicals' hypothesis) (Schmitz *et al.*, 1992; Sherbrooke, 1976) and the availability of alternative resources. The theoretical work of Emlen (1966) and MacArthur & Pianka (1966) also led to the prediction that resource selection by an animal should tend towards generalisation when food is scarce and towards specialisation when it is plentiful (Lacher *et al.*, 1982). An animal which is foraging optimally and ranking its food items in order of preference (Pulliam, 1975a) may 'switch' to less preferred species when the availability of highly preferred species becomes limiting (Murdoch, 1969).

The relative proportions of exploited seeds consumed *in situ* and removed from depots varied between seed species. The majority of *Sorbus* and *Ulmus* seeds were consumed *in situ* (66.5 and 60.1%, respectively), whereas the majority of *Betula*, *Fraxinus Ilex* and *Taxus* seeds were removed from depots (83.3, 83.2, 83.3 and 87.7%, respectively). With the exception of *Betula*, for which rates of seed encounter

averaged less than fifteen percent, small seeds with a low testa mass and energy content (*Sorbus* and *Ulmus*; Table 3.6) were consumed *in situ*, whereas large seeds with a high testa mass and energy content (*Fraxinus*, *Ilex* and *Taxus*; Table 3.6) were removed. Ashby (1967) also found that large seeds were more often removed from depots and small seeds more often consumed *in situ*. Such foraging decisions may reflect the relative handling times of different seed types, with respect to maximising rates energy intake and minimising predator exposure and energy expenditure.

Rates of encounter were proportionally greater for seeds of *Ulmus* in Shipley Wood and *Betula* in Derwent Gorge (Figure 3.4). As seeds presented in both sites were selected randomly from the same source, they were unlikely to have differed significantly in their physical and chemical characteristics. However, the relative value of these species at each site may have been influenced by their familiarity (Partridge, 1981), the dietary requirements of resident seed predators and the availability of alternative food resources. Seed encounter may have been disproportionately high if the seeds presented were either common or rare, relative to the natural availability of conspecific seeds, according to pro-apostatic or anti-apostatic selection, respectively (Soane & Clarke, 1973; Greenwood *et al.*, 1984a,b; Allen, 1988; Hulme & Hunt, 1999). Although the densities of adult *Betula* and *Ulmus* were greater in Shipley Wood (88.6 and 28.7 trees ha^{-1}, respectively) than in Derwent Gorge (10.0 and 8.1 trees ha^{-1}, respectively), the relative availability and familiarity of each taxon cannot be assessed without quantifying relative seed production in each study site.

Apostatic selection may also influence spatial patterns of seed predation. Beneath a fruiting adult tree, the predation of conspecific seeds may be either disproportionately high or low as a function of their relative frequency, assuming the appropriate search image can be formed. In tropical forests, close associations between plant species and host-specific seed predators, typically invertebrates, have been frequently recorded (Connell, 1971: Clark & Clark, 1984), with marked selection for conspecific seeds beneath fruiting adult trees. However, rodents are more often generalist foragers, particularly when the food supply is temporally or spatially unpredictable, consuming seeds opportunistically according to preference and availability (Drozdz, 1966; Murdoch, 1969). In the present study, there was no

evidence to support the selection or avoidance of conspecific seeds beneath adult trees, relative to seeds of other species. This may have resulted from the natural availability of seed beneath a fruiting adult being insufficient to invoke a predator search image for or against conspecific seeds. Alternatively, familiarity or apostatic selection of any kind may not be significant to rodents foraging under field conditions. The present study was not specifically designed to investigate patterns of frequency-dependent predation, rendering the drawing of any conclusions difficult.

3.4.4 **Variation between microhabitats**

Microhabitat variation has been consistently observed in studies of tree seed survival in temperate deciduous woodland (Table 3.1), with intense seed predation often separated by only a few metres from areas where seed loss was negligible (Webb & Willson, 1985; Willson & Whelan, 1990; Whelan *et al.*, 1991; Boman & Casper, 1995). This fine-scale spatial heterogeneity typically reflected patterns of rodent foraging in response to microhabitat characteristics, particularly the distribution of protective vegetation cover (Ashby, 1967; Gardner, 1977; Jensen, 1985; Webb & Willson, 1985; Wada & Uemura, 1994; Boman & Casper, 1995; Hulme, 1996a) and the abundance of seeds (Boman and Casper, 1995). Variation between sites has also attributed to differences in the availability of seeds (Watt, 1923) and vegetation cover (Jensen, 1982; Goldberg, 1985; Webb & Willson, 1985; Kollmann *et al.*, 1998).

The extent of vegetation cover may vary spatially and temporally according to the species of established plant. The dispersion of temperate forest plants has been principally attributed to physical habitat factors, such as soil quality, light intensity, microtopography and the depth of leaf litter (Bratton, 1976; Sydes & Grime, 1981; Crozier & Boerner, 1984). The availability of seeds in a microhabitat depends on the magnitude of seed input and the size of the seed bank. Factors influencing seed input include the distance from the seed supply, the size of the seed crop, the intensity of pre-dispersal predation and the efficiency of dispersal. Dispersal is likely to vary within and between sites according to wind exposure, patterns of water flow and the movements of animal dispersers. The size of the seed bank would depend on previous seed input and the survival of seeds in the soil. The quality of seeds arriving in a microhabitat would depend on the abundance of tree species with highly preferred seed within dispersal range.

In an attempt to maximise the benefits (e.g. dietary intake) and minimise the constraints (e.g. energy expenditure) on an animal's performance, optimal foraging theory would predict that foragers would select protected microhabitats with the greatest abundance of high quality food items. Vegetation cover and food availability are often correlated, although conflicts may arise between minimising predator exposure and energy expenditure, and maximising rates of energy intake (Lima *et al.*, 1985). Rodents may forage in open areas, of high predation risk, if they contain highly preferred food items (O'Dowd & Hay, 1980).

In the present study, patterns of microhabitat use varied significantly between treatments (Table 3.4, Figure 3.3) and sites (Tables 3.4 and 3.5, Figures 3.2 and 3.5). Rather than foraging randomly, seed predators made selective decisions regarding habitat suitability. In both sites, rodents and invertebrates showed similar patterns of seed exploitation across microhabitats, but distinct patterns of seed encounter (Figure 3.3). Invertebrate encounter was low across all microhabitats, particularly in the open, and was only greater than fifteen percent beneath High Vegetation.

Rodents foraged broadly across all microhabitats, although rates of encounter did vary significantly between them. The decrease in encounter from Shrub to High Vegetation and Open microhabitats was likely to reflect patterns of foraging in response to vegetation cover and food availability. The availability of highly preferred seeds beneath adults of *Corylus avellana* (Gurnell, 1993; Kollmann & Schill, 1996; Smal & Fairley, 1980; Jensen, 1985; Grodzinski & Sawicka-Kapusta, 1970) and the provision of low lying vegetation cover was likely to account for high rates of foraging in this microhabitat. Seeds of *Corylus* with characteristic rodent damage were frequently observed beneath fruiting adults, although seed production and predation were not quantified for this taxon. In contrast, Open microhabitats provided minimal cover and were some distance from any seed source. This may account for proportionally lower rates of seed encounter in open microhabitats, consistent with other studies of tree seed survival in temperate deciduous woodland (Table 3.1). Intermediate rates of encounter were observed in High Vegetation microhabitats, which were highly favourable in terms of vegetation cover, although were some distance from any seed source.

Rodent encounter was of a similar, high magnitude beneath adults of all study species (Figure 3.3). Rates of encounter were greatest beneath adults of *Ilex*, where

the provision of low lying vegetation cover and proximity to an exploitable seed supply would have been favourable. Wada and Uemura (1994) found that almost all seeds presented beneath shrub vegetation dominated by *Ilex crenata* var. *paludosa* were consumed *in situ*, where rodents were most active. It is important to note that despite showing well defined microhabitat preferences, rodents foraged over a broad range of microhabitat types. Even in less preferred microhabitats, rates of seed encounter and exploitation were often intense.

Patterns of microhabitat use varied significantly between sites (Figures 3.2 and 3.5). Seed encounter beneath adults of *Fraxinus* and exploitation beneath *Fraxinus* and *Ilex*, were proportionally greater in Shipley Wood. In contrast, seed encounter beneath High vegetation and exploitation beneath *Taxus* were proportionally greater in Derwent Gorge. Consistent with variation within sites, differences between sites were most likely a function of habitat suitability. Populations of *Fraxinus* differed between Shipley Wood and Derwent Gorge, both in the density and spatial distribution of adult trees. The density of adult *Fraxinus* was almost twice as great in Shipley Wood as in Derwent Gorge (91.6 and 49.1 trees ha^{-1}, respectively), with adult trees more associated with the lower regions of Shipley Wood and the middle regions of Derwent Gorge (Chapter 2). These differences, particularly in the density of adults, may account for variation in the relative value of *Fraxinus* microhabitats within each site. In addition, differences in canopy density, fruit production, seed dispersal and plant associations may have influenced relative habitat suitability, leading to differential foraging between sites.

Variation in these factors was also likely to account for the differential use of *Ilex*, *Taxus* and High Vegetation microhabitats. In both sites, patches of High Vegetation (*Pteridium aquilinum*) were associated with openings in the canopy, assuming soil suitability. In Derwent Gorge, patch size was generally smaller than in Shipley Wood. Depots placed in the centre of each patch would, therefore, be closer to adjacent adult trees at the perimeter of the patch. If the number of seeds of a given species arriving at any point in the woodland declined exponentially with increasing distance from the parent plant, seed input at depots beneath High Vegetation in Derwent Gorge may have been higher than in Shipley Wood, resulting in proportionally greater microhabitat use. The significance of this effect, however, would depend on the spatial scale of seed dispersal and rodent foraging, the

distribution of fruiting adult trees with respect to patches of High Vegetation and the size of their respective seed crops. Since patterns of seed rain in High Vegetation microhabitats were not quantified, such an effect can only be hypothesised. Alternatively, variation between sites may have resulted from differences in the availability of High Vegetation microhabitats. The extent of High Vegetation cover was greater in Derwent Gorge than in Shipley Wood, both at the beginning (percentage cover averaging 11-25% and <4%, respectively) and at the end of the experiment after dying back (percentage cover averaging <4% and 0%, respectively). This may account for the proportionally greater value of High Vegetation microhabitats in Derwent Gorge.

In Shipley Wood, the mean basal girth of adult *Ilex* was significantly lower than in Derwent Gorge (42.3 and 104.6cm, respectively; $t_{28} = 4.71$, $p<0.001$; Chapter 2). The shorter, shrubbier individuals of *Ilex* in Shipley Wood would have provided foraging rodents with improved low-lying vegetation cover, which may have led to proportionally greater use of this microhabitat. This may also account for greater rates of exploitation beneath adults of *Taxus* in Derwent Gorge, where the mean basal girth of individuals was significantly lower than in Shipley Wood (116.6 and 222.3cm, respectively; $t_{58} = 7.38$, $p<0.001$; Chapter 2). Differences in fruit production, seed dispersal and plant associations may have also contributed to variation between sites.

The absolute factors contributing to differential microhabitat use between sites are not easily distinguished, although variation most likely resulted from differences in the intrinsic quality of microhabitats in terms of food supply and vegetation cover.

Secondary to influencing patterns of microhabitat use, predation risk may have also constrained alternative foraging decisions. For example, handling time may have been of greater significance in the open than beneath protective vegetation cover, potentially reducing the number of seeds exploited '*in situ*'. This may favour seed removal to lower risk microhabitats, or may result in a shift in dietary preference towards food items with reduced handling requirements (Lima & Valone, 1986). Consequently, the maximisation of energy intake may be compromised in an attempt to minimise exposure to predators.

Across all microhabitats, an average of 37.8% of exploited seeds were consumed *in situ* and 62.2% were removed from depots. The relative proportion of seeds consumed *in situ* and removed was similar in the open (40.5 and 59.5%,

respectively) and variation between species in rates of encounter and exploitation was consistent between microhabitats. There was no marked shift in seed preferences in the open, despite increased predator exposure and handling time constraints. It is likely that rather than favouring seed removal over consumption *in situ*, or shifting seed preferences to species with reduced handling times, rodents responded to Open microhabitats with a lower intensity of foraging. This was reflected in rates of seed encounter averaging less than fifteen percent.

3.4.5 **Impact of seed predation on plant demography**

Consistent with previous studies of temperate deciduous woodland (Table 3.1), rates of post-dispersal seed predation recorded in the present study were extremely variable. This further demonstrates the difficulty in reaching general conclusions regarding the impact of seed predation on plant demography and evolution, which ultimately depends on the magnitude and consistency at which predation pressure is exerted and the ability of plants to compensate for losses or invest in anti-predator defence.

Although differential seed predation over a species' seed shadow has been found to influence spatial patterns of seedling emergence (Anderson, 1987; Harmon & Stamp, 1992), alternative factors including heterogenous patterns of seed rain (Herrera *et al.*, 1994), environmental requirements of seed germination, seedling establishment and plant survival (Callaway, 1992; Herrera *et al.*, 1994; Hulme 1996a) and spatio-temporal conflicts between seeds and seedlings (Houle, 1992; Schupp, 1995; Kollmann & Schill, 1996) may be of greater significance to ultimate patterns of plant recruitment and community composition.

CHAPTER 4

DISTANCE- AND DENSITY-DEPENDENT POST-DISPERSAL SEED PREDATION

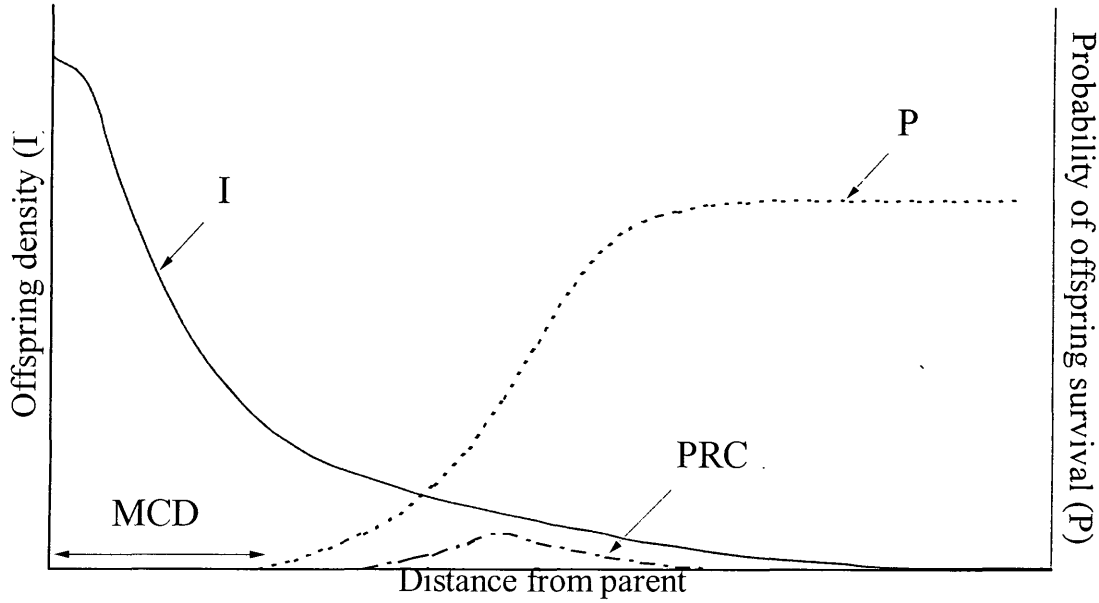
4.1 INTRODUCTION

4.1.1 **Studies of distance- and density-dependent post-dispersal seed predation**

Plants that regenerate from seed have a limited potential for independent movement. The dispersal of propagules away from the parent is, therefore, a significant component of the regeneration sequence. Local seed dispersal has a number of demographic benefits (Howe & Smallwood, 1982), particularly as a means of: a) expanding the geographic range of a population ('Colonisation Hypothesis'); b) locating favourable microhabitats which enhance seedling establishment and survival ('Directed Dispersal Hypothesis'); and c) escaping the detrimental effects of being close to the parent, which may include parental suppression, the association of disease vectors (Fox, 1977; DeSteven & Putz, 1984) or sibling competition where offspring density is at its highest (West, 1968) ('Escape Hypothesis'). Parental suppression may include shading (Horn, 1971; Clark & Clark, 1984), allelopathy (Tubbs, 1973, 1976; Horsely, 1977) and resource depletion (Zinke, 1962).

Janzen (1970) and Connell (1971) independently proposed that there may be disproportionately high offspring mortality beneath a parent plant resulting from the increased activity of herbivores. In this 'Herbivore Escape Hypothesis' (Figure 4.1), where offspring density (I) follows the primary seed dispersal curve, the probability of offspring survival (P) is lowest beneath the parent. Janzen (1970) and Connell (1971) proposed that this pattern may be generated by either 'Density-dependent' predators, responding to the high density of offspring beneath the parent, or 'Distance-dependent' predators, responding directly to the distance between the offspring and the parent plant, independent of density. It was hypothesised that vertebrates were more likely to be density-dependent, and invertebrates more likely distance-dependent. They also proposed that complete offspring mortality within some 'Minimum Critical Distance' (MCD) would generate a 'Population Recruitment Curve' (PRC) some distance from the parent (Figure 4.1). This would have a spacing effect, opening up the habitat for colonisation by other species, and has been hypothesised as a significant factor maintaining the high tree species diversity of tropical forests.

Figure 4.1. Graphical model of the 'Herbivore Escape Hypothesis', after Janzen (1970). The 'population recruitment curve' (PRC) peaks beyond some 'minimum critical distance' (MCD) from the adult, as a product of offspring density (I) and the probability of offspring survival (P).



Many studies evaluating the Janzen-Connell model have monitored the long-term survival of seedlings and saplings (reviewed in Clark & Clark, 1984). Alternatively, spacing mechanisms have been deduced from the spatial distribution of adult trees (Hubbell, 1979; Fangliang *et al.*, 1997; Itoh *et al.*, 1997). This may be inappropriate, however, since low offspring survival beneath the parent may be equally generated by sibling competition or parental suppression acting on seedlings and saplings. Such an investigation should, therefore, consider the post-dispersal survival of seeds, thus isolating the mechanisms of the herbivore escape hypothesis before these alternative processes come into effect.

Studies of density- and distance-dependent post-dispersal tree seed predation, across a range of tropical and temperate forest ecosystems, are reviewed in Table 4.1. Rodents were the major post-dispersal seed predator group in temperate deciduous woodland. In tropical forest, mammals and invertebrates, particularly insects, were the major post-dispersal seed predators in a similar number of studies (twelve and ten, respectively). Density-dependent predation has been directly investigated as frequently in temperate deciduous woodland as in tropical forest, whereas distance-dependent predation has been principally investigated in tropical forest. The range

Table 4.1. Review of studies investigating patterns of density- and distance-dependent tree seed predation in temperate and tropical woodland. Density ranges include the number of seeds presented in the area sampled. Depots were typically plastic petri-dishes or equivalent. Density- and distance-dependent seed predation is included unless otherwise stated - Seed encounter (Enc), Seed exploitation (Exp). Density and distance dependence were either positive (+), negative (–) or not significant (n.s.). Support for a minimum critical distance was either significant (+) or not significant (n.s.). Weaker evidence is shown in parentheses. Contrasting Local scale and Population (Pop^n) scale responses are included.

Source	Country	Major predator class	*Plant species*	Density range	Distance range (m)	Density dependence	Distance dependence	Evidence for MCD
Temperate deciduous woodland								
Jensen (1982)	Denmark	Rodents	*Fagus sylvatica*	0-346/1.0m^2		–		
Stapanian & Smith (1984)	USA	Rodents	*Juglans nigra*	6.25-100/1.0m^2		+		
			Quercus macrocarpa			+		
			Quercus muehlenbergii			+		
Jensen (1985)	Denmark	Rodents	*Fagus sylvatica*	2-25/0.1m^2		(+)		
Webb & Willson (1985)	USA	Rodents	*Prunus virginiana*	2- 40/depot	0-10	n.s.	–	n.s.
Willson & Whelan (1990)	USA	Rodents	*Cornus drummondii*	2-16/depot		+ Enc (–)Exp		
			Prunus serotina			+ Enc (–)Exp		
Hulme (1996a)	UK	Rodents	*Taxus baccata*	1-10/depot		n.s.		
Akashi (1997)	Japan	Rodents	*Fagus crenata*	10-380/1.0m^2	0-6	+	n.s.	n.s.

Table 4.1. Continued.

Source	Country	Major predator class	*Plant species*	Density range	Distance range (m)	Density dependence	Distance dependence	Evidence for MCD
Tropical forest								
Janzen (1972a)	Puerto Rico	Insects	*Euterpe globosa*	1-778/0.36m^2	3-5.5	n.s.	n.s.	(+)
Janzen (1972b)	Costa Rica	Insects	*Sterculia apetala*		1-130		–	+
Wilson & Janzen (1972)	Costa Rica	Insects	*Scheelea rostrata*	1-50/depot	0.5-8	+	n.s.	n.s.
				50/depot-308/0.24m^2		–		
Boucher (1981)	Costa Rica	Mammals	*Quercus oleoides*	1-500/5.0m^2		+ Local scale		
						– Pop^n scale		
Wright (1983)	Panama	Insects	*Scheelea zonensis*		1-16		n.s.	n.s.
					>100		–	n.s.
Forget (1992)	French-Guiana	Rodents/Insects	*Eperua grandiflora*		0-25		n.s.	n.s.
Schupp (1992)	Panama	Rodents	*Faramea occidentalis*		0-5	+ Local scale	–	n.s.
						– Pop^n scale		
Howe (1993)	Panama	Mammals	*Virola nobilis*		5-45		n.s.	n.s.
		Insects					–	n.s.
Terborgh *et al.* (1993)	Peru	Invertebrates	*Astrocaryum macrocalyx*		5-25		–	n.s.
		Mammals	*Bertholletia excelsa*		10-50		n.s.	n.s.
		Mammals	*Dipteryx micrantha*		10-50		n.s.	n.s.
		Mammals	*Hymenaea courbaril*		10-50		n.s.	n.s.
Burkey (1994)	Mexico	Rodents	*Brosimum alicastrum*	200-13200/1960m^2	1-25	–	–	n.s.
Notman *et al.* (1996)	Peru	Mammals/Insects	*Macoubea guianensis*	10/1.0m^2-10/depot	1-20	n.s.	n.s.	n.s.
			Pouteria sp.	5/1.0m^2-5/depot		n.s.	+	n.s.
Cintra (1997)	Peru	Mammals	*Astrocaryum murumuru*			+		
		Insects				–		
	Peru	Mammals/Insects	*Astrocaryum murumuru*	4-16/0.09m^2	0-20	+	n.s.	n.s.
			Dipteryx micrantha		0-40	n.s.	–	n.s.
Peres *et al.* (1997)	Brazil	Rodents	*Bertholletia excelsa*		5-35		n.s.	n.s.
					>300		–	n.s.

over which distance- and density-dependence were observed, varied between studies. Of the thirteen studies investigating patterns of distance-dependence, five sampled to distances of ten metres from the adult or less, and only three sampled to distances greater than fifty metres. Density ranges also considered responses at a small, local scale and at a broader, population scale.

Evidence for density- and distance-dependent seed predation is summarised in Table 4.2. Positive density-dependence, consistent with the herbivore escape hypothesis, was observed in only ten of a total of twenty-two cases. In a further six cases, predation intensity declined with increasing seed density. Negative distance-dependence, consistent with the herbivore escape hypothesis, was observed in only nine of the total twenty-two cases. In only a single case was distance-dependent seed predation sufficient to generate a clear minimum critical distance. An increase in predation intensity with distance from the parent was infrequent.

Table 4.2. Summary of evidence for density- and distance-dependent post-dispersal seed predation. The number of individual cases of significant positive (+) or negative (−) dependence, and the number cases where seed predation did not vary significantly (n.s.) with either density or distance, are shown. Positive and negative evidence for a minimum critical distance are also summarised. Parentheses include studies with partial evidence. Patterns of seed predation in temperate and tropical woodlands, and by invertebrate and mammalian seed predators, are distinguished.

	Density-dependence			Distance-dependence			MCD	
	+	–	n.s.	+	–	n.s.	+	n.s.
TOTAL	9(10)	6	6	1	9	12	1(2)	20
Temperate	4(5)	1	2	0	1	1	0	2
Tropical	5	5	4	1	8	11	1(2)	18
Invertebrate	1	2	1	0	4	3	1(2)	5
Mammal	7(8)	4	2	0	3	6	0	9

There was some evidence that patterns of density- and distance-dependence differed between temperate deciduous woodland and tropical forest. In temperate woodland, positive density-dependence, consistent with the herbivore escape hypothesis, was observed in the majority of cases, whereas in tropical forest, there were as many cases in which seed predation was either negatively or not significantly

density-dependent. Negative distance-dependence, consistent with the herbivore escape hypothesis, was more characteristic of seed predation in tropical forests, although at least as many observations found no significant variation with distance from the adult. Patterns of distance-dependence in temperate woodland cannot be distinguished from the limited number of observations to date.

Howe (1993), Terborgh *et al.* (1993) and Cintra (1997) directly distinguished patterns of density- and distance- dependence by alternative predator groups. Mammals were positively density-dependent and not significantly distance-dependent, whereas invertebrates were both negatively density and distance-dependent. Across all studies (Table 4.2), mammals more often showed positive density-dependence than any alternative, whereas invertebrates more often showed negative distance dependence and were responsible for both cases of 'minimum critical distance'. Although there were cases of negative distance dependence by mammals and positive density dependence by invertebrates, there is some evidence to support the hypothesis that vertebrates are more likely to be density-dependent and invertebrates more likely distance-dependent (Connell, 1971).

The majority of studies investigated the predation of only a single seed species. Of the five studies including more than one species, Terborgh *et al.* (1993), Notman *et al.* (1996) and Cintra (1997) found variation between species in patterns of density- and distance-dependence. Stapanian & Smith (1984) found that although the survival of black walnuts (*Juglans nigra*), bur oak acorns (*Quercus macrocarpa*) and chinquapin oak acorns (*Q. muehlenbergii*) decreased with increasing nut density, lower densities of walnuts were more easily distinguished by rodents, as a result of their greater odour concentration.

Wilson & Janzen (1972), Boucher (1981) and Schupp (1992) found that at low seed densities, seed predation was positively density-dependent, consistent with the herbivore escape hypothesis. However, at a population level, high seed densities satiated seed predators and increased seed survival. Jensen (1982) and Burkey (1994) also found that seed predation was negatively and linearly related to total seed production. Scale was also significant to distance-dependence. Peres *et al.* (1997) and Wright (1983) found that at a local scale, seed removal did not vary significantly with distance from the adult. However, at a population scale, there was a marked decline in

seed removal at distances greater than three hundred and one hundred metres, respectively. In contrast, Webb & Willson (1985) found that predation risk was markedly reduced beyond a distance of only two metres from the adult.

From investigations to date, it is difficult to conclusively support the herbivore escape hypothesis, with patterns of distance- and density-dependence inconsistent between plant species and predator groups, across a range of forest ecosystems. In addition patterns were often scale-dependent, with processes at the level of an individual tree not necessarily representative of processes at the population level. Hubbell (1980) questioned the validity of distance- and density-dependence on theoretical grounds alone, recognising the paradox between the intense post-dispersal seed predation recorded beneath parent trees and the spatial aggregation of adult populations in tropical forest. The discrepancy was believed to lie in the scaling of axes in Janzen's (1970) original graphical model (Figure 4.1). The omission of numerical axes failed to consider that offspring density (I) was unbounded, whereas the probability of offspring survival (P) was confined to the range between zero and one. Hubbell (1980) concluded that maximum offspring density and population recruitment would occur at the parent, even though relative offspring survival may increase with distance the tree.

It is clearly difficult to make general predictions regarding the benefits of seed dispersal and the impact of density- and distance-dependent seed predators on spatial patterns of plant recruitment and species diversity.

4.1.2 **Study aims**

The majority of studies reviewed in Table 4.1, investigated either the density- or distance-dependent predation of a single seed species by a single predator group. The principle aim of this study was to examine both density- and distance-dependent seed predation, for a range of native tree species and predator groups. The potential impact of seed predation on spatial patterns of plant recruitment and species diversity will be discussed.

The specific aims of the study were to;

1. Determine whether seed predators respond to seed density (density-dependent predation).

2. Assess variation in seed survival with distance from the parent (distance-dependent predation).

3. Examine whether patterns of density- and distance-dependence differ significantly between tree species, and between vertebrate and invertebrate seed predators.

4.2 MATERIALS AND METHODS

4.2.1 **Design of field trials**

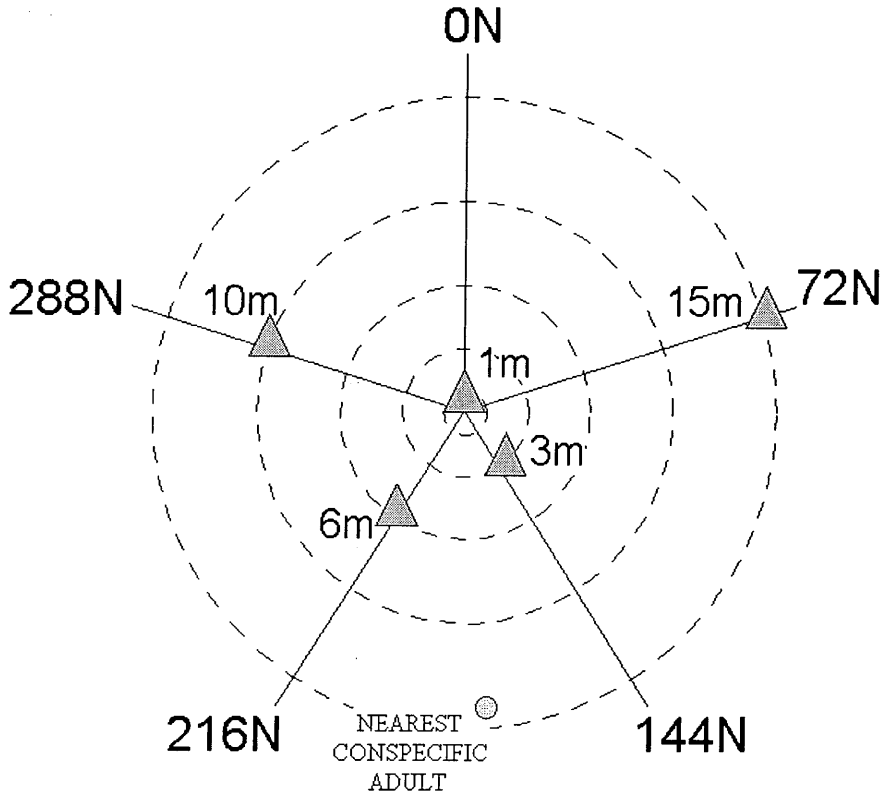
Patterns of distance- and density-dependent seed predation were investigated in Shipley Wood. The study species included taxa that differed in seed size, fruiting time, dispersal mechanism and adult density (Table 3.3); *Fraxinus*, *Ilex*, *Sorbus*, *Taxus* and *Ulmus*. Seeds were presented at sampling points comprising 'Invertebrate', 'Rodent' and 'Open' treatment types, as described in Chapter 3. Sampling points were placed at distances of 1, 3, 6, 10 and 15 metres from the base of ten replicate adult trees of each study species. Trees of a similar size were selected from across the site, at least ten metres from the nearest conspecific adult to minimise interference. Sampling points were positioned along one of five transects projecting from each replicate tree at 0, 72, 144, 216 and 288 degrees north (Figure 4.2). This allocation was random where possible, although constrained to ensure that sampling points were always at a greater distance from the nearest conspecific adult than from the replicate adult. The orientation of different distance sampling points varied between replicate adult trees.

Seed predation trials were conducted during the natural fruiting period of each taxon; *Fraxinus* (22nd April-1st May, 1996), *Ulmus* (21st-30th June, 1996), *Taxus* (28th September-7th October, 1996), *Sorbus* (10th-19th November, 1996), *Ilex* (27th January-5th February, 1997). Trials were repeated for *Fraxinus* the following year (4th-13th March, 1997), when there was an abundance of fruit production. Trials were not conducted for *Betula*, since background depletion of the seed supply to wind and rain was excessively high during the fruiting period. The vast number of naturally dispersed seeds falling beneath fruiting adults also made it impossible and unrealistic to monitor the survival of single seeds presented during trials.

Seeds presented during trials were collected from adult trees at the time of fruit maturation and seed dispersal (Chapter 3). For each tree species, conspecific seeds were presented at each dish at a randomly selected density of 1, 5 or 10 seeds. Within each sampling point, treatments received the same density of seeds during each trial. After three days, the number of seeds remaining intact was recorded, giving a measure of seed predation. Seed removal was assumed to result in seed death, through either consumption away from the depot or dispersal to unfavourable germination microsites. Seed remains were then cleared from each depot and the seed

supply replenished with that of an alternative density. Trials continued until every sampling point had received seed at each density.

Figure 4.2. Schematic diagram showing the arrangement of sampling points (▲) along experimental transects projecting from each replicate adult tree, as constrained by the locality of the nearest conspecific adult (●). Transects were orientated in degrees north (N) and sampling points were positioned at distance intervals from one to fifteen metres.



4.2.2 **Statistical analysis**

Seed predation data were analysed following Hulme (1994a), distinguishing seed encounter from seed exploitation, as described in Chapter 3. Since distance, seed density, exclosure treatment and seed species were all fixed effects, seed encounter and exploitation data were most appropriately analysed using a 'fixed model' or 'Model I' factorial analysis of variance in GLIM, assuming a binomial error distribution (Zar, 1984; NAG, 1985).

Analysis was undertaken simultaneously on data from all species, to identify overall patterns of variation according to treatment, seed species, seed density and distance from a conspecific adult. Seeds at density one were omitted from the analysis of exploitation data, as single seeds would not have permitted intermediate rates of

exploitation once encountered. Factorial analysis of variance (Model I) was also conducted separately for each study species in order to distinguish individualistic patterns of distance- and density-dependence.

The spatial association between rates of seed encounter and exploitation at Rodent and Open depots was determined from the Yates corrected Chi-squared statistic for seed encounter and the Pearson sample correlation coefficient for seed exploitation (Chapter 3), on the arcsine transformed proportion of seeds exploited.

4.3 RESULTS

4.3.1 **Seed encounter**

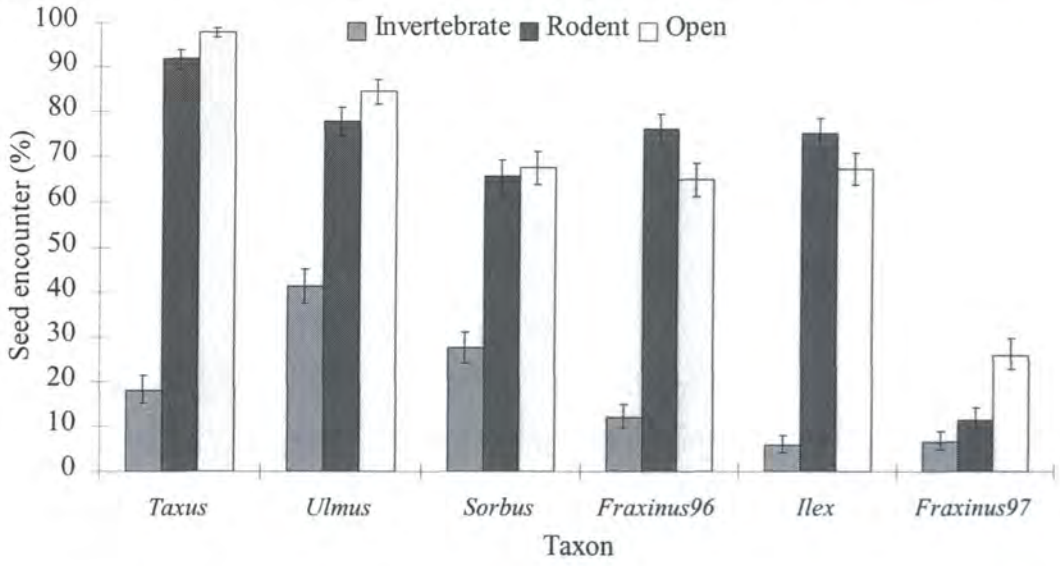
4.3.1.1 Variation between treatments and species

Rates of seed encounter varied significantly between treatments, between species and within taxa for *Fraxinus* in two years, and variation between species was treatment dependent (Table 4.3, Figure 4.3). Rates of encounter at Rodent and Open depots were highly spatially correlated (χ^2 =294.24, df=1, p<0.001) and variation between species was broadly similar. Seed encounter was greater than sixty-five per cent for all taxa except *Fraxinus* in 1997, with seeds of *Taxus* most frequently encountered. The encounter of *Fraxinus* seeds was significantly greater in 1996 than in 1997 (t_{296}=15.487, p<0.001 and t_{296}=7.712, p<0.001, for Rodent and Open treatments, respectively). In contrast, Invertebrate encounter was only greater than twenty percent for seeds of *Ulmus* and *Sorbus*. *Fraxinus* seed encounter was low in both 1996 and 1997, and the encounter of *Taxus* and *Ilex* was proportionately lower than at Rodent and Open depots.

Table 4.3. Total variation in seed encounter partitioned between the main effects (species, treatment, distance and density) and their higher order interactions. Significance levels (p) were ≥0.05 (n.s., not significant), <0.05 (✶), <0.01 (✶✶) and <0.001 (✶✶✶).

Source	df	SS	MS	F	p
Species (sp)	5	375.10	75.02	81.76	✶✶✶
Treatment (tr)	2	695.50	347.75	378.99	✶✶✶
Distance (di)	4	7.10	1.77	1.93	n.s.
Density (de)	2	53.99	26.99	29.42	✶✶✶
sp.tr	10	117.80	11.78	12.84	✶✶✶
sp.di	20	61.92	3.10	3.37	✶✶✶
sp.de	10	21.52	2.15	2.35	✶
tr.di	8	9.63	1.20	1.31	n.s.
tr.de	4	4.13	1.03	1.13	n.s.
di.de	8	4.27	0.53	0.58	n.s.
sp.tr.di	40	47.18	1.18	1.29	n.s.
sp.tr.de	20	18.71	0.94	1.02	n.s.
sp.di.de	40	27.59	0.69	0.75	n.s.
tr.di.de	16	7.93	0.50	0.54	n.s.
sp.tr.di.de	80	51.14	0.64	0.70	n.s.
Residual	2412	2213.20	0.92		
Total	2681	3716.80	1.39		

Figure 4.3. Mean percentage seed encounter (± 1 S.E.) of each species, for each treatment.



4.3.1.2 *Density-dependent seed encounter*

Rates of seed encounter varied significantly with seed density (Table 4.3). Patterns of density-dependence were similar between treatments and between distances, but differed significantly between species (Table 4.3, Figure 4.4). Analysis was conducted separately for each species in order to distinguish patterns of density-dependence (Table 4.4). Single seeds of *Taxus*, *Sorbus* and *Fraxinus* in 1997 were encountered significantly less frequently than seeds at greater densities, consistent with the herbivore escape hypothesis. The encounter of *Ulmus*, *Ilex* and *Fraxinus* seeds in 1996 was not density-dependent.

The density dependent encounter of *Sorbus* was similar in all three treatments ($F_{4,399}$ = 0.889, p>0.05), with open depots reflecting patterns of rodent and invertebrate encounter. In contrast, there was a significant interaction between treatment and density for the encounter of *Taxus* ($F_{4,402}$ = 5.513, p<0.001). Seed encounter at rodent depots increased significantly with seed density (Figure 4.5), consistent with the herbivore escape hypothesis. However, this pattern was not reflected in overall rates of seed encounter at Open depots, and even at density one, seed encounter approached ninety percent. Invertebrate encounter varied significantly, although there was no clear trend with seed density. Although there was no significant interaction between density and treatment ($F_{4,402}$ = 0.388, p>0.05), the encounter of *Fraxinus* seeds by invertebrates in 1997 was not density dependent, with rates of encounter consistently less than 10% (Figure 4.6).

Figure 4.4. Mean percentage seed encounter (± 1 S.E.) of each species, at each density.

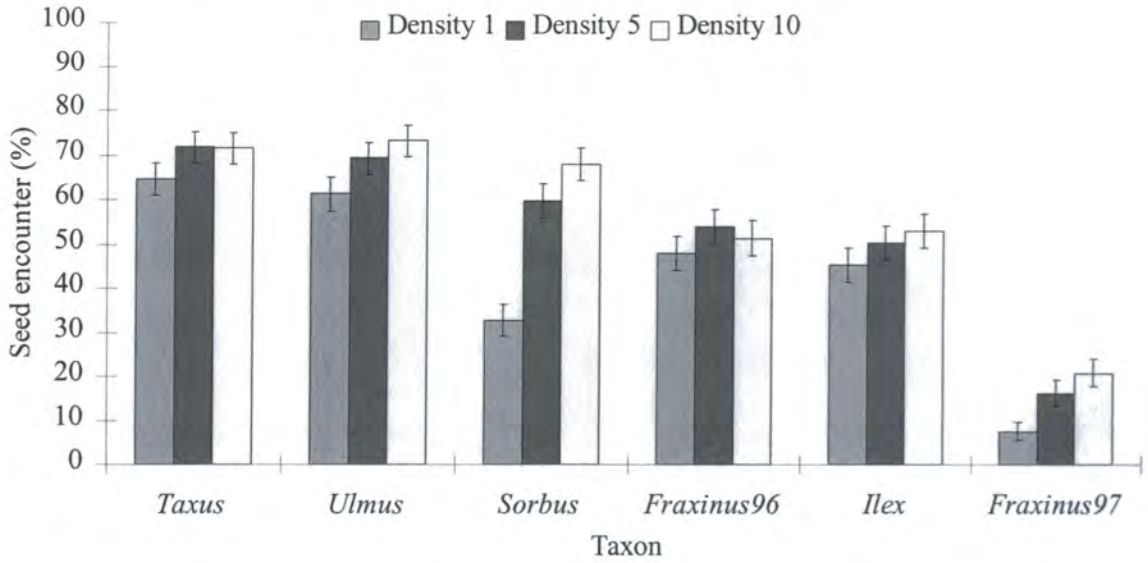


Table 4.4. Patterns of density- and distance-dependent seed encounter for each study species. Results of factorial analysis of variance include the significance and direction of each association (+, positive relationship; – negative relationship; n.s., no significant variation).

Taxon	Density-dependence		Distance-dependence	
*Fraxinus*96	**n.s.**	$F_{2,401}=0.770$ $p \geq 0.05$	**n.s.**	$F_{4,401}=2.776$ $p \geq 0.05$
*Fraxinus*97	+	$F_{2,402}=8.492$ $p <0.001$	**n.s.**	$F_{4,402}=2.414$ $p \geq 0.05$
Ilex	**n.s.**	$F_{2,403}=1.784$ $p \geq 0.05$	–	$F_{4,403}=5.076$ $p < 0.01$
Sorbus	+	$F_{2,399}=21.113$ $p <0.001$	**n.s.**	$F_{4,399}=0.600$ $p \geq 0.05$
Taxus	+	$F_{2,402}=7.173$ $p <0.01$	+	$F_{4,402}=13.622$ $p < 0.001$
Ulmus	**n.s.**	$F_{2,405}=2.717$ $p \geq 0.05$	**n.s.**	$F_{4,405}=0.449$ $p \geq 0.05$

Figure 4.5. Mean percentage encounter (± 1 S.E.) of *Taxus* seeds at each density, for each treatment.

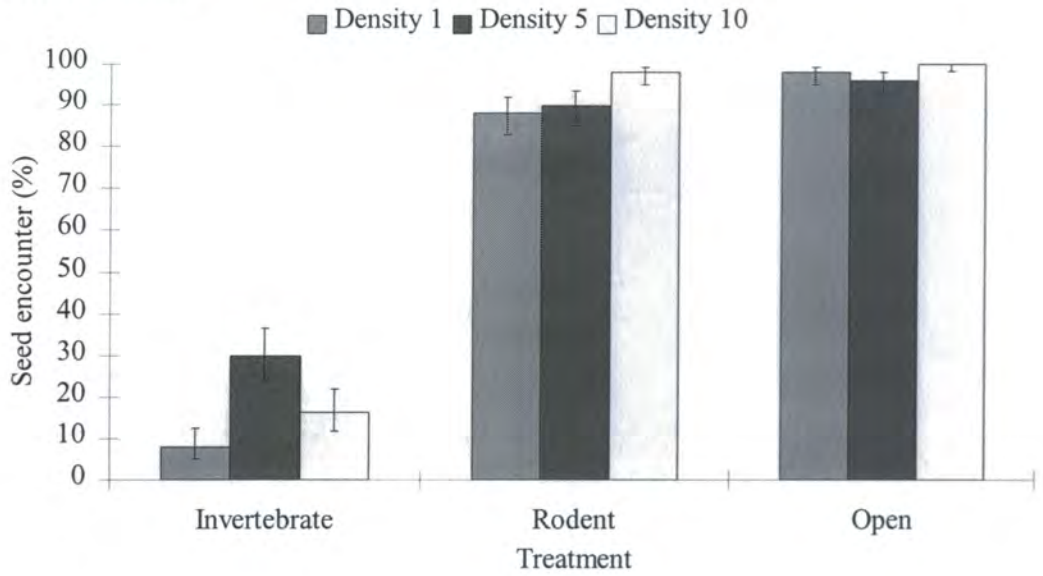
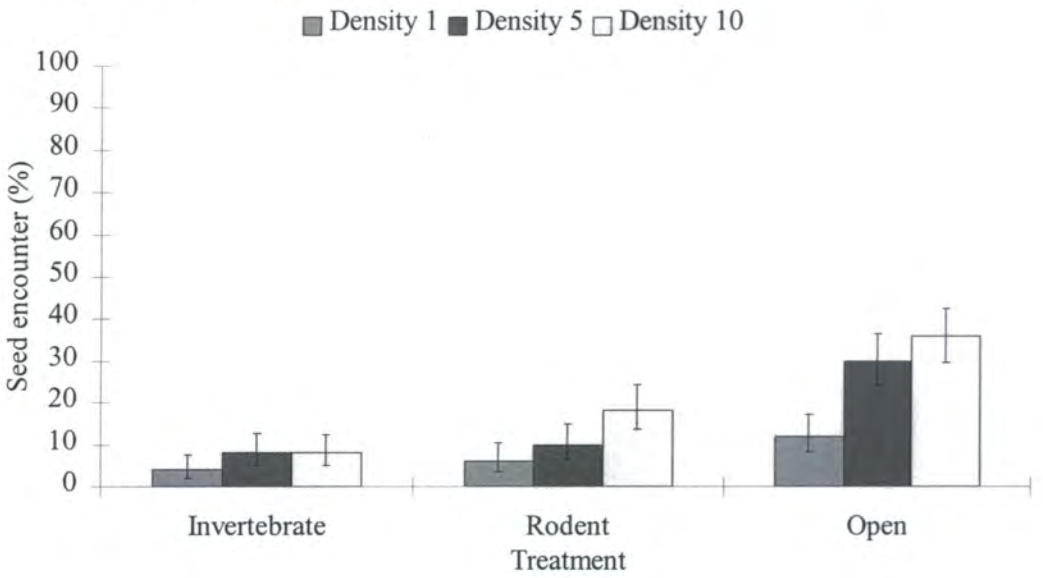


Figure 4.6. Mean percentage encounter (± 1 S.E.) of *Fraxinus* seeds at each density, for each treatment in 1997.



4.3.1.3 *Distance-dependent seed encounter*

Patterns of distance-dependent seed encounter were similar between treatments, but varied significantly between species (Table 4.3). Analysis was conducted separately for each species in order to distinguish these patterns. The encounter of *Sorbus*, *Ulmus* and *Fraxinus* in both years, did not vary significantly with distance from the adult, for any of the treatments (Table 4.4). *Ilex* and *Taxus* seed

encounter were distance-dependent, according to treatment ($F_{8,403}$ = 2.299, p<0.05, Figure 4.7 and $F_{8,402}$ = 3.240, p<0.01, Figure 4.8, respectively).

The encounter of *Ilex* seeds at Open depots declined significantly with increasing distance from the adult. This trend was consistent with the herbivore escape hypothesis and was supported by negatively distance-dependent encounter at Rodent depots. However, the negative distance-response at Open depots was only significant at a small spatial scale, where seed encounter was significantly greater directly beneath the adult than at three metres (t_{178}=2.187, p<0.05) and beyond. Invertebrate encounter generally increased with distance, although was at a sufficiently low magnitude not to influence the overall response. At both rodent and invertebrate depots, *Taxus* seed encounter increased significantly with distance from the parent, opposite to that predicted by the herbivore escape hypothesis. However, these patterns were not reflected in overall rates of seed encounter at Open depots, which were consistently greater than ninety percent. There were no higher order interactions between species, treatment, distance and density (Table 4.3).

Figure 4.7. Mean percentage encounter (± 1 S.E.) of *Ilex* seeds at each distance from the parent.

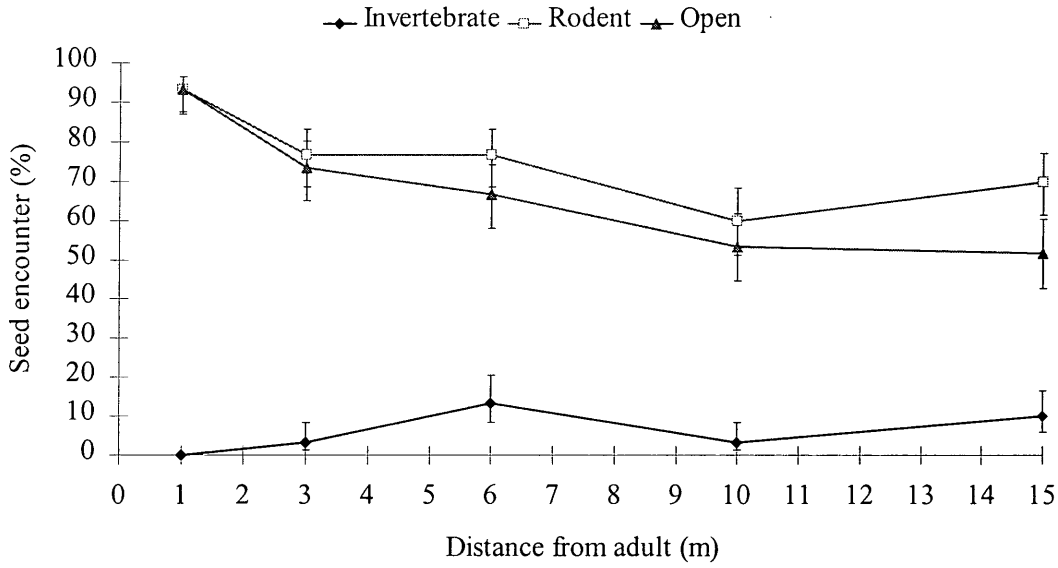
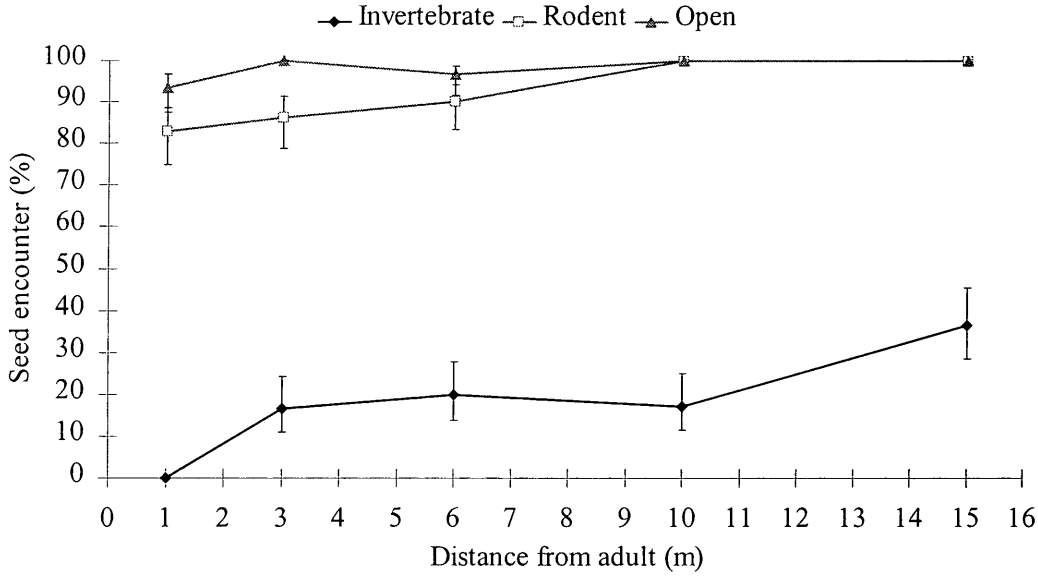


Figure 4.8. Mean percentage encounter (± 1 S.E.) of *Taxus* seeds at each distance from the parent.



4.3.2 **Seed exploitation**

4.3.2.1 *Variation between treatments and species*

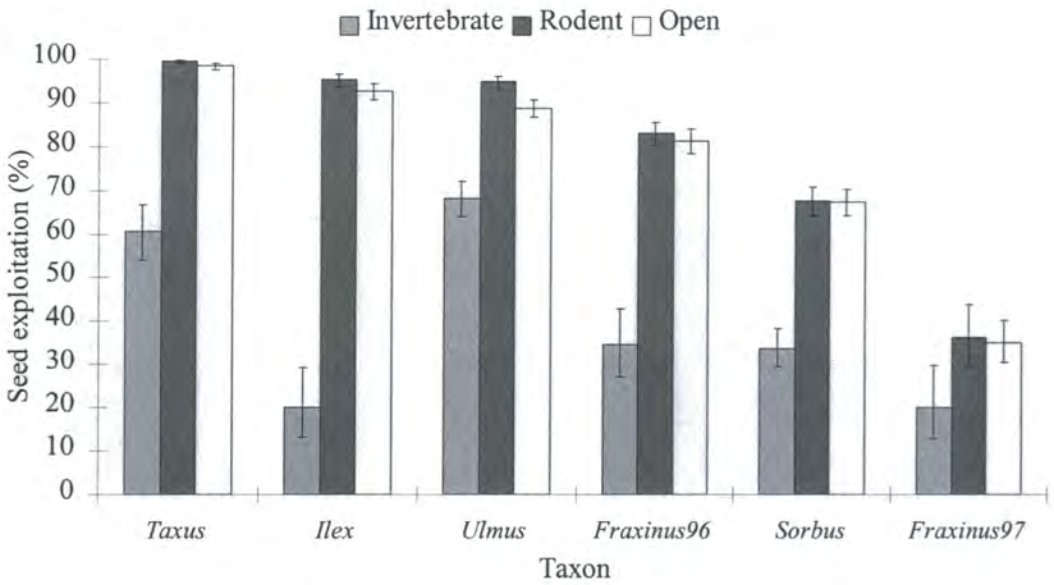
Rates of seed exploitation varied significantly between treatments, between species and within taxa for *Fraxinus* in two years, and variation between species was treatment dependent (Table 4.5, Figure 4.9). Rates of exploitation at Rodent and Open depots were highly spatially correlated (r_{363}=0.542, p<0.01), variation between species was similar and the rank order of species was the same. With the exception of *Fraxinus* in 1997, once encountered, the majority (>60%) of seeds of each taxon was exploited. Seeds of *Taxus* were most frequently exploited and *Fraxinus* seed exploitation was significantly greater in 1996 than in 1997 (t_{90}=6.041, p<0.001 and t_{97}=8.172, p<0.001, for Rodent and Open treatments, respectively).

Invertebrate exploitation was substantial relative to rates of invertebrate encounter, although it was only greater than thirty-five percent for seeds of *Taxus* and *Ulmus*. Exploitation was proportionally higher for *Taxus* and *Ulmus*, and lower for *Ilex*, relative to the other two treatments. The exploitation of *Fraxinus* seeds by invertebrates was of a similar low magnitude in both years (t_{898}=1.274, p>0.05).

Table 4.5. Total variation in seed exploitation partitioned between the main effects (species, treatment, distance and density) and their higher order interactions. Significance levels were ≥0.05 (n.s., not significant), <0.05 (✶), <0.01 (✶✶) and <0.001 (✶✶✶).

Source	df	SS	MS	F	*p*
Species (sp)	5	1178	235.6	88.491	✶✶✶
Treatment (tr)	2	623.0	311.5	116.999	✶✶✶
Distance (di)	4	13.42	3.355	1.260	n.s.
Density (de)	1	0.832	0.832	0.312	n.s.
sp.tr	10	162.1	16.21	6.088	✶✶✶
sp.di	20	111.8	5.59	2.100	✶✶
sp.de	5	13.28	2.656	0.998	n.s.
tr.di	8	35.58	4.4475	1.670	n.s.
tr.de	2	3.791	1.8955	0.712	n.s.
di.de	4	19.88	4.97	1.867	n.s.
sp.tr.di	36	101.0	2.8056	1.054	n.s.
sp.tr.de	10	7.785	0.7785	0.292	n.s.
sp.di.de	20	88.5	4.425	1.662	n.s.
tr.di.de	8	11.00	1.375	0.516	n.s.
sp.tr.di.de	31	42.51	1.37129	0.515	n.s.
Residual	817	2175.2	2.662		
Total	983	4587.9			

Figure 4.9. Mean percentage seed exploitation (± 1 S.E.) of each species, for each treatment.



4.3.2.2 *Density-dependent seed exploitation*

Seed exploitation was not density-dependent, for any of the species, treatments or distances investigated.

4.3.2.3 *Distance-dependent seed exploitation*

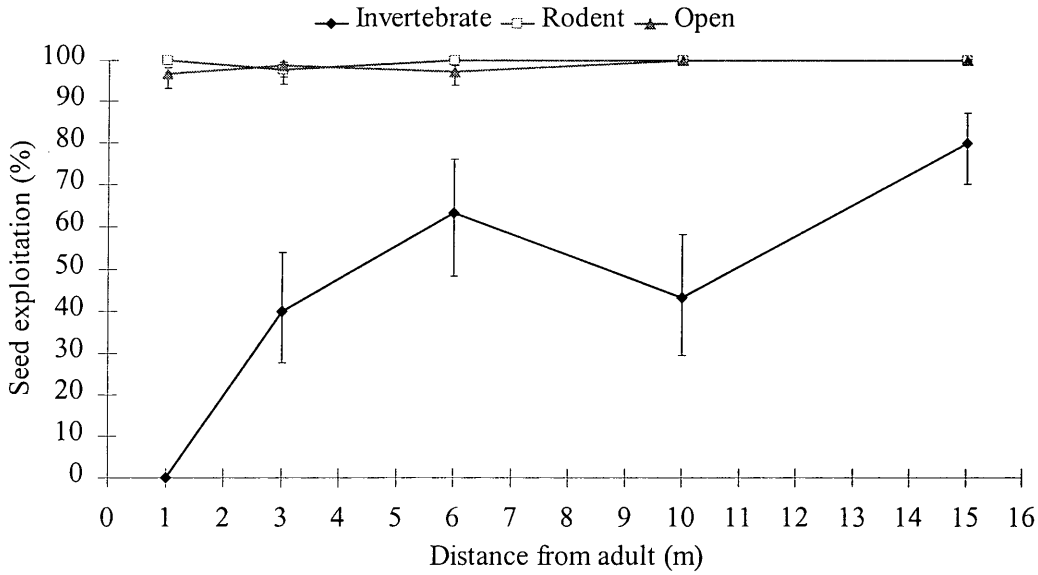
Patterns of distance-dependent seed exploitation were similar between treatments, but varied significantly between species (Table 4.5). Analysis was conducted separately for each species in order to distinguish these patterns. The exploitation of *Ilex*, *Sorbus*, *Ulmus* and *Fraxinus* in both years, did not vary significantly with distance from the adult, for any of the treatments (Table 4.6). *Taxus* seed exploitation was distance-dependent, according to treatment ($F_{7,185}$=3.287, p<0.01; Figure 4.10). At Rodent and Open depots, *Taxus* seed exploitation was consistently greater than ninety-six per cent, whereas invertebrate exploitation varied markedly. There was no clear relationship between rates of exploitation and distance from the adult, for any of the treatments. There were no higher order interactions between species, treatment, distance and density (Table 4.5).

Table 4.6. Patterns of distance-responsive seed exploitation for each study species. Results of factorial analysis of variance include the significance of each association (✶, significant variation, no relationship; n.s., no significant variation).

Taxon	Distance-dependence	
*Fraxinus*96	**n.s.**	$F_{4,130}$=2.006 $p \geq 0.05$
*Fraxinus*97	**n.s.**	$F_{4,30}$=0.280 $p \geq 0.05$
Ilex	**n.s.**	$F_{4,128}$=1.851 $p \geq 0.05$
Sorbus	**n.s.**	$F_{4,160}$=1.225 $p \geq 0.05$
Taxus	✶	$F_{4,185}$=8.910 p <0.001
Ulmus	**n.s.**	$F_{4,184}$=2.336 $p \geq 0.05$

At rodent and open depots, the rates of encounter of each species were positively correlated with the rates of exploitation (r=0.954, df=4, p<0.01 and r=0.913, df=4, p<0.01, respectively). Species that were most frequently encountered were also most frequently exploited. At invertebrate depots, rates of encounter and exploitation were not significantly correlated (r=0.786, df=4, p=n.s.).

Figure 4.10. Mean percentage exploitation (± 1 S.E.) of *Taxus* seeds at each distance from the parent, for each treatment.



4.3.3 **Impact of predator groups**

Consistent with the previous study of seed predation (Chapter 3), molluscs (including *Arion* spp. and *Agiolimax* spp.) were the only invertebrates and rodents (including *Clethrionomys glareolus*) the only mammals seen feeding at dishes. This was supported by the presence of faeces, mucus and seed remains at dishes which were characteristic of each group. Birds were seen consuming fruit from canopies of *Ilex*, *Taxus* and *Sorbus*, but were not observed foraging on seeds at experimental depots.

4.4 DISCUSSION

4.4.1 **Impact of predator groups**

Rates of encounter and exploitation were of a similar high magnitude at Rodent and Open depots, where seed species were ranked in a similar order (Figures 4.3 and 4.9). In addition, patterns of encounter and exploitation at Rodent and Open depots were highly spatially correlated. Background seed loss and that attributable to invertebrates were significantly lower than the other two treatments. Rodents were, therefore, considered to be the principal agents responsible for seed encounter and exploitation, with patterns of distance- and density-dependence largely reflecting rodent foraging behaviour.

4.4.2 **Variation between tree species**

Rates of encounter and exploitation varied significantly between species and within species, according to treatment (Figures 4.3 and 4.9). Species that were most frequently encountered by rodents (at rodent and open depots) were also most frequently exploited. Rates of encounter and exploitation were greatest for seeds of *Taxus*, *Ulmus* and *Ilex*, least for seeds of *Fraxinus* in 1997 and intermediate for seeds of *Sorbus* and *Fraxinus* in 1996.

As described in Chapter 3, variation between tree species most likely reflected the olfactory conspicuousness, handling time and nutritional value of each seed species, according to rodent seed preferences and the availability of protective vegetation cover beneath conspecific adult trees. Natural seed availability and the population density of rodents at the time of each experiment would have also varied between study species, as may have the level of activity of rodents.

Variation between species was generally consistent with patterns identified in Chapter 3. Variable rates of *Fraxinus* seed encounter and exploitation by rodents most likely reflected the natural abundance of *Fraxinus* seeds. In 1997, low rates of encounter and exploitation coincided with abundant fruit production averaging over 1.1 million *Fraxinus* seeds per hectare. Encounter and exploitation were significantly greater in 1996, when the natural availability of *Fraxinus* seeds was low. This would support 'masting' as a mechanism of satiating rodent seed predators and increasing the probability of conspecific seed survival (Boucher, 1981; Jensen, 1982; Schupp, 1992). Invertebrate seed predators did not respond to variation in the natural

abundance of *Fraxinus* seeds. The relative influence of rodent density and the availability of vegetation cover could not be assessed in the absence of survey data.

4.4.3 **Variation with seed density**

Seed density influenced the probability of encounter (Stapanian & Smith, 1984), rather than exploitation, although variation in seed survival with seed density was species dependent (Cintra, 1997). Density-dependent encounter, consistent with the herbivore escape hypothesis, was principally supported by *Sorbus* and *Fraxinus* in 1997 (Figure 4.4, Table 4.4). Density-dependent seed exploitation was not substantially supported by any of the seed species or treatments.

Rodents were the principal agents responsible for the density-dependent encounter of *Fraxinus* seeds. Patterns of density-dependence varied according to spatial scale (Wilson & Janzen, 1972; Boucher, 1981; Schupp, 1992) and local food abundance (Willson & Whelan, 1990). When the natural availability of *Fraxinus* seeds was low in 1996, seed encounter at a local scale did not vary significantly with seed density, for any of the treatments (Figure 4.4, Table 4.4). In 1997, coinciding with an abundance of fruit production, the encounter of *Fraxinus* seeds was positively density-dependent, consistent with the herbivore escape hypothesis. This was likely to reflect a shift from generalist foraging when seed availability was low, to more selective foraging when seeds were abundant (Emlen, 1966; MacArthur & Pianka, 1966; Lacher *et al.*, 1982). At a population level, rodents were satiated by mast seeding (Jensen, 1982; Burkey, 1994), resulting in proportionally greater seed survival and negative density-dependence. Contrasting local (positive) and population level (negative) density-dependence was consistent with Boucher (1981) and Schupp (1992).

Single seeds of *Sorbus* were encountered significantly less frequently than seeds at higher densities. Rates of encounter and exploitation were similar at densities five and ten. Rodents and invertebrates showed similar patterns of density-dependence. Density-dependent seed survival may be influenced by seed size (Mittelbach & Gross, 1984). Hulme (1993) suggested that predation on small seeds was more likely to be density-dependent than predation on large seeds. Of the taxa investigated in the present study, seeds of *Sorbus* were of the lowest mass (Table 3.3) and rates of encounter were most consistently density-dependent. However, it was difficult to disassociate the influence of seed size from alternative habitat parameters,

including the availability of protective vegetation cover and alternative food, including conspecific seeds, and the population density of seed predators competing for resources at the time of each experiment.

It is significant that negative evidence only disproved density-dependent encounter and exploitation for the density range considered in the investigation. Across alternative density ranges, Wilson & Janzen (1972) found contrasting density-dependence (Table 4.1). Across a low density range, seed predation increased with seed density, whereas, across a high density range, seed predation decreased with seed density as predators became satiated. The encounter of *Fraxinus* seeds in the present study supported such contrasting local and population scale responses to seed density. Considering scale-dependence, general conclusions regarding patterns of density-dependence should be made with some caution.

4.4.4 **Variation with distance from the adult**

Distance from the adult influenced the probability of seed encounter (Stapanian & Smith, 1984), rather than exploitation, although variation in seed survival with distance from the adult was species dependent (Terborgh *et al.*, 1993; Notman *et al.*, 1996; Cintra, 1997). Distance-dependent encounter, consistent with the herbivore escape hypothesis, was principally supported by *Ilex* (Figure 4.7, Table 4.4). Distance-dependent seed exploitation was not substantially supported by any of the seed species or treatments (Table 4.6).

The encounter of *Ilex* seeds was significantly greater directly beneath conspecific adult trees than at greater distances (Figure 4.7). Rodents were the principal agents responsible for this trend. Preferential foraging beneath adults of *Ilex* was consistent with patterns of seed predation recorded in Chapter 3. *Ilex* microhabitats were considered most beneficial in terms of protective vegetation cover and food supply. Although this distance response was consistent with the basic principle of the herbivore escape hypothesis, it occurred over such a small spatial scale that it was not meaningful in terms of the spacing mechanisms hypothesised by the Janzen-Connell model. However, short-term seed survival would have been enhanced by dispersal of only a few metres from the parent (Webb & Willson, 1985) although even at a distance of fifteen metres, rodent encounter exceeded fifty percent.

As with density-dependent effects, negative evidence only disproved distance-dependent encounter and exploitation at the spatial scale considered. Across

alternative distance ranges, Wright (1983) and Peres *et al.* (1997) found contrasting distance-dependence. In both cases, seed predation did not vary significantly with distance at a local scale (0-16 and 5-35 metres, respectively), but decreased significantly with distance at a population scale (>100 and >300 metres, respectively). Again, considering scale dependence, general conclusions regarding patterns of distance-dependence should be reached with some caution.

In the present study, there was no evidence for any species that seed survival increased significantly beyond some 'minimum critical distance', at least over the distance range investigated. However, an average of 98 and 99 per cent of all artificially supplied *Taxus* seeds were encountered and exploited, respectively, after only three days of exposure to all categories of seed predator. In addition, not a single naturally dispersed *Taxus* seed was found to have escaped predation beneath the fruiting adults investigated. Although there was no evidence that *Taxus* seed survival increased at distances beyond those sampled, it was clear that at least local recruitment was likely to have been significantly limited by post-dispersal seed predation, particularly by rodents. In the study described in Chapter 3, seeds of *Taxus* were most preferred of all the taxa and rates of seed loss were high in all microhabitats sampled. In addition, seedlings of *Taxus* were encountered very infrequently during surveys of Shipley Wood (Chapter 6). A dramatic increase in seed survival beyond some minimum critical distance from the parent was, therefore, unlikely. Lack of evidence for any of the study species was consistent with the majority of woodland studies investigating distance-dependent tree seed predation (Table 4.1).

4.4.5 **Variation within tree species**

Rates of *Fraxinus* seed encounter and variation with seed density differed significantly according to the natural availability of conspecific seeds. In fact, variation within species was greater than variation between species. Other tree species may show equal temporal dynamics in total rates of seed encounter and exploitation, and in patterns of distance- and density-dependence. In Shipley Wood, fruiting adults of *Fraxinus* were at a high density and seed production varied dramatically between years. In addition, the encounter and exploitation of *Fraxinus* seeds were low when seeds of more preferred taxa were available (Chapter 3). Only in the spring of 1996,

when the natural availability of seeds of all taxa was low, were seeds of *Fraxinus* encountered and exploited at high rates. Although seed production was not formally quantified over the study period, it was apparent that fruiting adults of the other species were of low abundance and produced smaller, more regular crops of preferred seed. Under such conditions, the potential for predator satiation is limited (Boucher, 1981) and temporal variation in patterns of distance- and density-dependence, according to the availability of conspecific seeds, are likely to be less extreme.

4.4.6 **Variation between predator groups**

Studies which directly distinguished patterns of density- and distance-dependence by alternative predator groups, found that mammals were positively density-dependent, whereas invertebrates were both negatively density and distance-dependent (Howe, 1993; Terborgh *et al.,* 1993; Cintra, 1997). Across all studies of density- and distance-dependent post-dispersal seed survival (Table 4.2), mammals more often showed positive density-dependence than any alternative, whereas invertebrates more often showed negative distance-dependence.

In the present study, mammalian and invertebrate seed encounter were positively density-dependent for two and one of the five species investigated, respectively. Mammalian and invertebrate seed encounter was negatively distance-dependent for one and none of the five species investigated, respectively. Seed exploitation was not density- or distance-dependent for any of the treatments. There was no evidence to support the hypothesis that vertebrates were more likely to be density-dependent and invertebrates more likely distance-dependent (Connell, 1971).

4.4.7 **Evaluation of the 'Herbivore Escape Hypothesis'**

The variability of post-dispersal seed predation has been a consistent factor in all of the studies in which it has been investigated. Variation in space, between sites and microhabitats, in time, between seasons and years, and according to seed burial, seed frequency, seed species and predator group are described in Chapter 3. In the present study, the effects of seed density and distance from the adult on post-dispersal seed survival, varied significantly between and within tree species. Mixed support was consistent with other studies of density- and distance-dependent seed survival, across a range of continents, habitats, plant species and predator groups, (Table 4.1). In all studies, negative evidence only disproved density- or distance-dependent

predation for the size-age class considered in the investigation, across the density or distance range sampled.

Patterns of density- and distance-dependent seed survival are largely unpredictable and can not be generalised temporally or spatially for alternative plant species and predator groups. For many plant species, seed dispersal may be an effective and necessary means of escaping disproportionately high seed predation beneath the parent, which may ultimately influence spatial patterns of recruitment and species diversity. Alternatively, seed dispersal may be a necessary means of escaping seedling herbivory, parental suppression or sibling competition beneath the parent. For other species, seed dispersal may be more significant in terms of colonisation and directed dispersal, where the impact of seed predation may be secondary to spatio-temporal conflicts between seeds and seedlings (Houle, 1992; Schupp, 1995; Kollmann & Schill, 1996) and the environmental requirements of seed germination, seedling establishment and plant survival (Callaway, 1992; Herrera *et al.*, 1994; Hulme, 1996a). In the absence of spacing mechanisms hypothesised by the Janzen-Connell model, species diversity may be maintained by the suppression of single species dominance by opportunistic, frequency-dependent seed predators (Murdoch, 1969; Connell, 1971).

In the present study, there was marginal support for the hypothesis that seed predation was more likely to be density-dependent in temperate woodland and distance-dependent in tropical forest. Density-dependent seed survival was supported by two of five tree species, whereas distance-dependent survival was not supported by any species at a spatial scale consistent with the herbivore escape hypothesis. Rodents were the principal seed predators, foraging throughout the woodland and consuming a mixed diet, including seeds of numerous tree species (Chapter 3). In the absence of host specificity, generalist and opportunistic post-dispersal seed predators are unlikely to respond directly to distance from the adult, independent of seed density. Distance-dependent predation is more likely to depend on the host-specificity of seed predators in tropical forest (Janzen, 1970).

Under theoretical conditions, disproportionately high offspring mortality beneath the parent may be sufficient to generate a spacing effect (Figure 4.1). However, in natural populations, with overlapping seed shadows, mortality-mediated spacing is much less predictable. For example, an increase in the distance to which

seeds were dispersed would result in a flattening of the seed shadow curve, assuming seed crop size remained constant. If seed densities were low throughout the dispersal range, close to the minimum threshold for predator search, the probability of seed survival may be equal at any distance from the parent, leading to random spacing in adult populations. In the present study, adults of *Fraxinus* were randomly distributed in both sites and adults of *Acer* and *Ilex* were randomly distributed in Derwent Gorge (Table 2.3). All other adult populations of the study species were spatially aggregated in the study sites, supporting the absence of predictable spacing mechanisms mediated by distance- and density-dependent seed predation.

Variation in seed crop size, the population density of seed predators and dispersers, and the availability of alternative food are also likely to generate a temporally dynamic association between post-dispersal seed predation and tree spacing (Hubbell, 1980). Alternative microhabitat characteristics, such as the availability of protective vegetation cover (Ashby, 1967; Gardner, 1977; Jensen, 1985; Webb & Willson, 1985; Wada & Uemura, 1994; Boman & Casper, 1995; Hulme, 1996a), may be ultimately more significant to patterns of rodent foraging than either seed density or distance from the parent.

CHAPTER 5

SEEDLING HERBIVORY

5.1 INTRODUCTION

5.1.1 **Studies of seedling herbivory**

Tree seedlings are particularly vulnerable following germination, when seed reserves have been depleted and seedlings first rely on the products of their photosynthesis for growth and survival. Studies of seedling survival have typically documented the many abiotic factors limiting post-germination survival, including desiccation, frost heaving, shade and litterfall, unfavourable seedbed conditions, flooding, fire and disturbance (Bramble & Goddard, 1942; Streng *et al.*, 1989; Gill & Marks, 1991; Reader, 1993; Jones *et al.*, 1994). Biotic factors limiting seedling growth and survival include competition (Goldberg, 1985; Gill & Marks, 1991), fungal attack (Streng *et al.*, 1989; Augspurger, 1984) and herbivory (Table 5.1). Relative to the vast literature detailing patterns of predator-mediated seed mortality, few studies have directly quantified the consumption of seedlings by herbivores, and the majority of these have been observational rather than experimental.

Studies of tree seedling herbivory in temperate deciduous woodland, across a range of countries, are reviewed in Table 5.1. The majority of studies followed the survival of naturally dispersed native tree seedlings (seedling survey, N). When mortality factors were not readily distinguished and the habitat contained a mixed suite of seedling herbivores, the experimental design was modified (M) to selectively restrict access to seedlings. Wire mesh exclosures, of appropriate gauge, were typically incorporated to quantify the relative impact of alternative herbivore groups. These groups may differ markedly in rates of herbivory, temporal and spatial scales of foraging, species and microhabitat preferences and their relative impact on plant recruitment. Alternatively, trials monitored the survival of transplanted nursery seedlings (T) or field germinated seedlings (F), derived from artificially planted seeds within 'experimental plots'. Sixty per cent of the studies considered only a single plant species, with less than fifteen per cent including more than three species.

High, variable rates of seedling herbivory were consistently observed. Of the eighteen studies reviewed, rodents and invertebrates were the principal seedling herbivores in eight and seven studies, respectively, and were of minor importance in a

Table 5.1. Review of studies investigating the survival of tree seedlings in temperate deciduous woodland. [1]Duration of trials in weeks unless otherwise stated. [2]Seedling herbivory (%) - Percentage of seedlings damaged by herbivores, unless otherwise stated. (L%) Percentage of leaves defoliated (1-100% leaf area lost). Methods of investigation include seedling surveys (S) and experimental plots (P). Modified treatments (M) restricted access to specific predator groups. Trials monitored the survival of naturally dispersed seedlings (N), transplanted nursery seedlings (T) and field germinated seedlings (F) from artificially planted seed. Rates of seedling herbivory varied according to De, seedling density; Di, distance from adult; M, microhabitat; Pr, category of seed predator; S, site; Sp, species of seedling and T, time of experiment (season/year). [3]Data taken from Golley *et al.* (1975).

Source	Country	Methods	Plant species	Duration of trial (wks)[1]	Major herbivore class	Seedling herbivory (%)[2]	Source of variation						
							De	Di	M	Pr	S	Sp	T
Bramble & Goddard (1942)	USA	P (F, M)	*Pinus rigida*	78	Rodents/Birds	4-60			+	+			
Humphrey & Swaine (1997b)	UK	P (T)	*Quercus petraea* *Q. robur x Q. petraea*	2	Insects	8-55 (L%)			+		+	(+)	
Maeto & Fukuyama (1997)	Japan	P (F)	*Acer mono*	5-6	Insects	0-56	+						
Pigott (1985)	UK	P (T+N, M)	*Betula pubescens* *Carpinus betulus* *Quercus petraea*	13	Rodents	0 0 73					+	+	
Rousi *et al.* (1996)	Finland	P (T)	*Betula papyrifera* *B. maximowicziana* *B. alleghaniensis* *B. pendula* *B. resinifera* *B. ermanii* *B. platyphylla*	Winter-Spring	Rabbits	95 88 88 78 62 40 30				+		+	
Watt (1923)	UK	P (T+N, M)	*Fagus sylvatica*	15-20	Insects/Molluscs	35-100				+	+		
Wood (1938)	USA	P (F)	*Quercus montana*	1 day/Winter	Rabbits	→100 / 28							

Table 5.1. Continued.

Source	Country	Methods	Tree species	Duration of trial (wks)[1]	Major herbivore class	Seedling herbivory (%)[2]	Source of variation						
							De	Di	M	Pr	S	Sp	T
Akashi (1997)	Japan	S	*Fagus crenata*	24	Rodents/Deer	0-90	+/n.s	n.s					
Dinesman (1961) [3]		S	*Acer* sp.		Rodents	25						+	
			Carpinus betulus			32							
			Quercus sp.			41							
Linhart &Whelan (1980)	UK	S	*Acer pseudoplatanus*	Winter-April	Sheep	67						+	
			Fraxinus excelsior			11							
Nakashizuka *et al.* (1995)	Japan	S	*Carpinus tschonoskii*		(Insects/Rodents)	7-14	n.s.	+					
Paterson *et al.* (1996)	UK	S	*Acer pseudoplatanus*	6	Molluscs	10-90			+	+			+
Peterken (1966)	UK	S	*Ilex aquifolium*		Rodents/Deer	→100			+				
Sviridenko (1940) [3]		S	*Quercus* spp.		Rodents	80-100						+	
			Ulmus spp.			80-100							
			Acer spp.			80-100							
			Tilia spp.			80-100							
			Fraxinus spp.			50-60							
			Sorbus aucuparia			50-60							
			Corylus spp.			0-20							
			Prunus padus			0-20							
Wardle (1959)	UK	S	*Fraxinus excelsior*	16	Insects	50							
Watt (1919)	UK	S (M)	*Quercus* sp.	≤ 35	Rodents	1-29				+	+		
Wood (1938)	USA	S	*Quercus* spp.		Insects	→100						+	+
			Quercus alba			23							
			Quercus montana			29							
			Quercus velutina			3							
Zhukov (1949) [3]		S	*Quercus* sp.		Rodents	51							

further three and one studies, respectively. Insects and molluscs were the most significant invertebrate groups. Rabbits, birds, deer and sheep were the principal seedling herbivores in fewer studies, although rates of herbivory were similar in terms of magnitude and variability. A number of studies directly quantified the relative impact of alternative herbivore groups, which were found to vary significantly in rates of seedling herbivory.

Although herbivores often destroyed all available seedlings, the majority of studies recorded extreme variation in rates of seedling herbivory relative to parameters associated with the environment, the resources and the herbivore guild.

All studies investigating more than one plant species found significant variation between species in rates of seedling herbivory, although such variation has rarely been accounted for. Wood (1938) found that herbivory varied between species according to the time of germination. Since most seedling damage occurred in winter, species that germinated in spring were able to escape herbivory. Herbivore resistance may also reflect investment in physical or chemical defence. In an investigation of the growth and resistance to hares (*Lepus timidus*) of *Betula* spp. seedlings, Rousi *et al.* (1996) found that highly resistant species contained high concentrations of phenolics, papyriferic acid and other related terpenoids.

Spatial variation in seedling herbivory was significant in a number of studies, where microhabitat variation reflected the behaviour of seedling herbivores. Consistent with spatial patterns of seed predation (Chapter 3), the survival of unprotected seedlings was greater in open microhabitats than in woodland or beneath dense vegetation, owing particularly to the reduced activity of small mammals (Bramble & Goddard, 1942; Peterken, 1966). Other studies recorded greater herbivory beneath a conspecific canopy than beneath adults of other species, reflecting some degree of host specificity (Paterson *et al.*, 1996; Humphrey & Swaine, 1997b; Maeto & Fukuyama. 1997).

Variation in seedling herbivory between sites may also reflect the activity and population density of seedling herbivores. Pigott (1985) found that differences between sites were correlated with rodent density, as determined by characteristics of the vegetation. Watt (1919) recorded significantly lower rates of seedling herbivory on clay (18.9%) than on sandy soil (28.6%), when seedlings were unprotected.

Rabbits were thought to prefer sandy soil to clay soil, which was considered an unsuitable substrate for colonisation and breeding. Humphrey & Swaine (1997b) also found that differences between sites in the defoliation of *Quercus* seedlings were positively correlated with the degree of infestation by lepidopteran larvae.

Density-dependent seedling herbivory has been infrequently investigated. Pigott (1985) found that seedling herbivory was negatively correlated with density, reflecting the satiation of rodent herbivores. In contrast, Akashi (1997) found a positive density-response, although seedling mortality patterns varied according to the spatial and temporal scale. Nakashizuka *et al.* (1995) found that the herbivory of *Carpinus tschonoskii* seedlings was not significantly density-dependent.

Distance-dependent seedling herbivory has also been observed (Nakashizuka *et al.*, 1995). Maeto & Fukuyama (1997) found that the herbivory of *Acer mono* seedlings by invertebrates decreased with distance from the parent, consistent with the 'herbivore escape hypothesis' (Chapter 4). In contrast, Akashi (1997) found that the herbivory of *Fagus crenata* seedlings by mammals was not significantly distance-dependent.

Paterson *et al.* (1996) found that the intensity of seedling herbivory was greater for seedlings that germinated later in the study. This may have resulted from increased slug activity, following a seasonal temperature rise, or a preference for younger, more palatable seedlings containing reduced levels of tannins. Insect damage may also vary seasonally, such that species germinating when most damage occurs are less likely to escape herbivory than species germinating at other times (Wood, 1938).

The loss of seedlings to herbivores is likely to limit the reproductive potential of many plant species. In addition, light herbivory may reduce the growth and competitive ability of seedlings (Hendrix, 1988). Extreme variation in rates of herbivory, according to plant and herbivore species, time, space and seedling density, have been inadequately accounted for, making general conclusions difficult regarding the impact of seedling herbivores on patterns of plant recruitment. The influence of variable and unpredictable patterns of seedling herbivory on plant demography and the evolution of anti-herbivore defence is also difficult to assess from current knowledge. To ensure the regeneration and persistence of plant species, it is clearly

fundamental to appreciate patterns of seedling herbivory and the potential for spatial and temporal escape, across a range of plant species and microhabitats.

5.1.2 **Study aims**

Following an initial investigation of post-dispersal seed predation, the principal aim of this study was to quantify the herbivory of recently germinated seedlings and examine variability with respect to plant community composition, spatial patterns of plant recruitment and the natural regeneration of temperate deciduous woodland.

The specific aims, for a range of native tree species, were to;

1. Quantify the relative impact of vertebrate and invertebrate herbivores on the survival of tree seedlings in temperate deciduous woodland.
2. Determine whether seedling herbivory varied significantly between species and examine the association between species preferences and seedling attributes.
3. Determine whether seedling herbivory varied spatially, across a range of microhabitats.
4. Examine whether vertebrate and invertebrate seedling herbivores differ in their species preferences and microhabitat use.
5. Examine the consistency of species preferences between microhabitats.

5.2 MATERIALS AND METHODS

Seedling herbivory was investigated in Shipley Wood, where the dynamics of natural seedling abundance had been monitored in a concurrent survey (Chapter 6). The study species included taxa that differed in seedling size, time of germination, adult density and patterns of seed predation: *Acer*, *Betula*, *Fraxinus*, *Ilex*, *Sorbus*, *Taxus* and *Ulmus*.

5.2.1 **Nursery practice**

Seedlings presented during trials were established from seeds collected from the study site. Seeds were collected from adult trees of each species at the time of fruit maturation and seed dispersal (Chapter 3). Pre-germination treatments, including scarification, soaking and stratification, were used to enhance germination success (Schopmeyer, 1974). The hard endocarps of *Ilex* and *Taxus* seeds were mechanically scarified using a Waring® Blender, until endocarps were visibly scarred. All seeds were then soaked in water for forty-eight hours prior to sowing and rinsed thoroughly of any germination inhibitors. Seeds were sown in mulched beds at a density and depth consistent with Schopmeyer (1974)(Table 5.2). The total number of seeds necessary to yield sufficient seedlings for the experimental design, varied between species according to seed viability (Table 5.2; Chapter 3).

To account for delayed germination, seeds were planted in each of the two years (November 1995 and 1996) prior to field trials in spring/summer 1997. Seed trays were placed outside for winter stratification, open to the environment and raised sufficiently above the ground to prevent access to rodent seed predators. Following germination, seedlings were watered regularly until the time of field presentation.

Table 5.2. Sowing depth, sowing density and seed viability of each species germinated. Nursery practice recommended by Schopmeyer (1974) is highlighted.

Taxon	Sowing depth (in.)	Sowing density (ft^{-2})	Seed viability (%)
Betula	**1/16-3/16**	**25-45**	13
Fraxinus	**1/4-3/4**	**10-15**	89
Ilex	**1/8-1/2**	15-25	58
Sorbus	**1/16**	15-25	94
Taxus	**3/8-1/2**	15-25	100
Ulmus	1/4-1/2	15-25	38

5.2.2 **Design of field trials**

Seedlings were presented at sampling points comprising 'Invertebrate', 'Rodent' and 'Open' treatment types, as described in Chapter 3. Five replicate sampling points were placed in each of the nine representative microhabitats sampled during seed predation trials; beneath adult *Betula*, *Fraxinus*, *Ilex*, *Sorbus*, *Taxus* and *Ulmus*, beneath Shrub (*Corylus avellana*) and High Vegetation (*Pteridium aquilinum*) and in the Open.

As a result of unpredictable seed germination, it was necessary to modify the experimental design. Seedlings of *Sorbus* and *Taxus* were entirely omitted from predation trials, following poor germination, and seedlings of *Acer* subsequently included. *Acer* seedlings were carefully harvested from a natural source and transplanted to seed trays until field presentation. The yield of *Ilex* seedlings was also insufficient for the complete experimental design, such that seedlings could only be presented in eight of the nine microhabitats sampled. *Ilex* seedlings were not presented beneath adults of *Taxus*, since *Taxus* had been entirely omitted from predation trials following poor germination.

Field presentation of seedlings followed the natural emergence of conspecific seedlings in Shipley Wood; *Acer* (19th April-1st May), *Fraxinus* (28th May-9th June), *Betula* (10th-22nd June), *Ilex* (25th June-7th July), *Ulmus* (9th-21st July). At the time of presentation, all seedlings were less than one month old, with cotyledons and their first pair of true leaves. Intact seedlings of a similar size were carefully transplanted from seed trays in the field. Single seedlings of each species were presented at each experimental depot. After three days, the number of seedlings remaining intact was recorded. Seedling damage was categorised according to the proportion of seedling remaining. Five categories represented progressively greater seedling damage; (1) 91-99% remaining, (2) 76-90% remaining, (3) 51-75% remaining, (4) 26-50% remaining, (5) 1-25% remaining, (6) complete consumption of the seedling.

Since the encounter and damage of all species was low after three days of exposure, trials were extended to permit greater exploitation of the resources. Rates of seedling encounter and damage were recorded at further three-day intervals until trials were terminated after twelve days of exposure. This period coincided with the earliest occurrence of wilting, to which seedlings of *Acer* were most sensitive. Seedling

remains were then removed from each depot and replaced by an alternative species. Trials continued until every sampling point had received each species of seedling.

5.2.3 **Analysis of seedling characteristics**

Growth, allocation and leaf characteristics of each species were determined. Saturated masses of total plants, total true leaves, total cotyledons, epicotyls, hypocotyls and roots were measured from ten seedlings of each species prior to field presentation, from which average masses per seedling were determined. Total leaf dry mass, total plant dry mass and total leaf plus cotyledon dry mass were then calculated from leaf saturated mass to dry mass ratios, leaf mass fractions (total leaf dry mass/total plant dry mass) and leaf plus cotyledon mass fractions (total leaf plus cotyledon dry mass/total plant dry mass) taken from Cornelissen *et al.* (1996). Mean relative growth rates for seedlings of each species (*sensu stricto*, excluding cotyledons from plant weight) were also taken from Cornelissen *et al.* (1996).

5.2.4 **Statistical analysis**

Data analysis considered two alternative components of seedling herbivory: seedling encounter (the probability of seedling herbivory) and seedling damage (the extent of seedling herbivory, once encountered). Seedling encounter was a binary variable, where seedlings were either encountered or not encountered. Microhabitat, treatment and species were all fixed effects, thus seedling encounter was most appropriately analysed using a 'fixed model' or 'Model I' factorial analysis of variance in GLIM, assuming a binomial error distribution (Zar, 1984; NAG, 1985). Variation in categorical seedling damage data was analysed using chi-squared analysis, according to microhabitat, treatment and species. Damage categories were pooled when necessary to fulfil the conditions of analysis regarding unity and the lower limit of expected frequencies. The inclusion of incomplete data from *Taxus* microhabitats did not significantly influence patterns of variation in seedling encounter and damage, between species, microhabitats and treatments.

For each treatment, seedling characteristics (total seedling dry mass, total leaf plus cotyledon dry mass, leaf saturated mass:dry mass ratio, leaf plus coyledon mass fraction and mean relative growth rate) were examined in relation to the mean proportion of seedlings encountered, using Pearson sample correlations, and the median severity of seedling damage, using Spearman rank correlations.

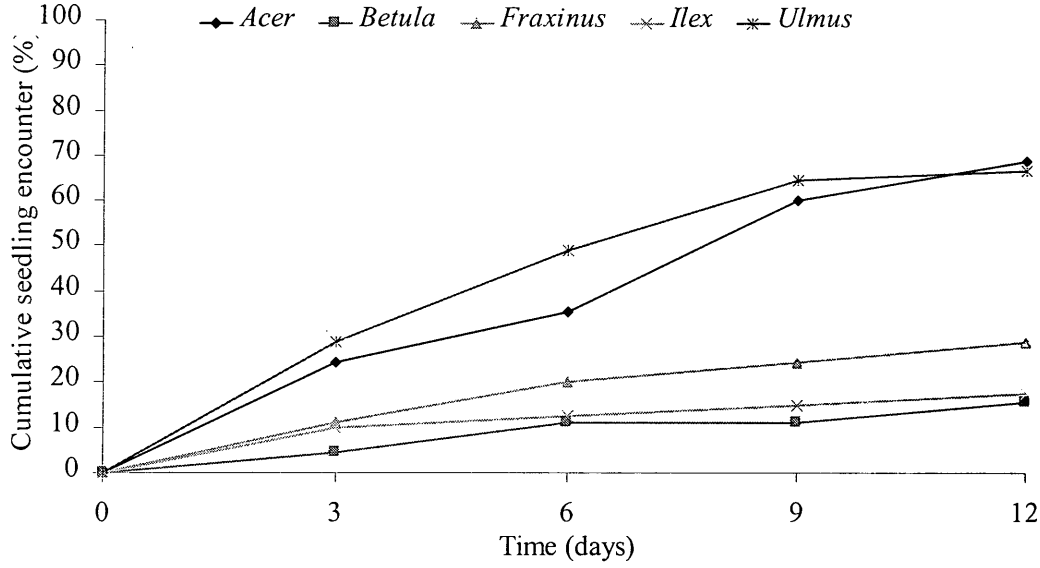
The spatial association between rates of seedling encounter and damage at Invertebrate, Rodent and Open treatments was determined from the Yates corrected Chi-squared statistic for seedling encounter and the Spearman Rank Correlation Coefficient for seedling damage.

5.3 RESULTS

5.3.1 **Seedling encounter**

After three days of exposure at Open depots, seedlings of all species were encountered at rates of less than thirty percent (Figure 5.1). The encounter of all species increased until trials were terminated after twelve days of exposure, at the earliest occurrence of wilting. The encounter of *Acer* and *Ulmus* was consistently greater than the encounter of *Betula*, *Fraxinus* and *Ilex*, and this was accentuated over the trial period. Further analysis will, therefore, consider patterns of seedling encounter and damage at the termination of each trial, reflecting a maximum period of exposure prior to wilting.

Figure 5.1. Cumulative percentage seedling encounter at Open depots, for each species over the trial period.



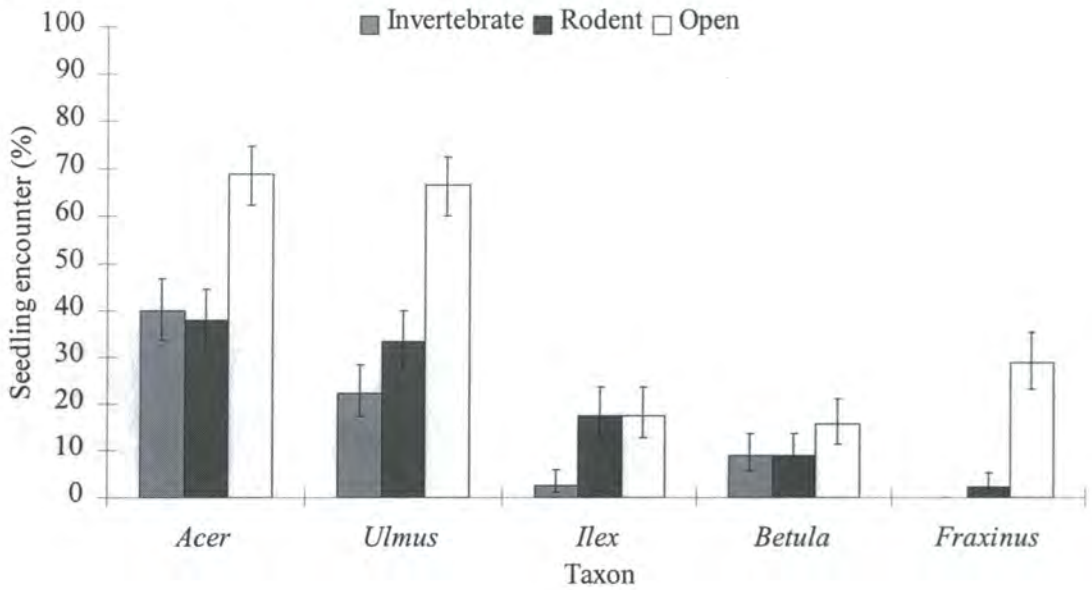
After twelve days of exposure, rates of seedling encounter varied significantly between treatments and between species, and variation between species was treatment dependent (Table 5.3, Figure 5.2). At Invertebrate, Rodent and Open depots, seedlings of *Acer* and *Ulmus* were more frequently encountered than seedlings of *Ilex*, *Betula* and *Fraxinus*. Treatments differed principally in the encounter of *Acer*, *Ulmus* and *Fraxinus* seedlings, which was proportionally higher at Open depots, and the encounter of *Ilex* seedlings, which was proportionally lower at Invertebrate depots. Seedlings of *Betula* were infrequently encountered (<20%) at all treatments. Seedling encounter at Open depots was highly spatially associated with rates of encounter at

Invertebrate (χ^2_{corr}=10.233, df=1, p<0.01) and Rodent (χ^2_{corr}=7.388, df=1, p<0.01) depots. There was no spatial association between rates of seedling encounter at Invertebrate and Rodent depots (χ^2_{corr}=0.804, df=1, p>0.05).

Table 5.3. Total variation in seed encounter (across all treatments) partitioned between the main effects (species, microhabitat and treatment) and their higher order interactions. Significance levels (p) were ≥0.05 (n.s., not significant), <0.05 (✶), <0.01 (✶✶) and <0.001 (✶✶✶).

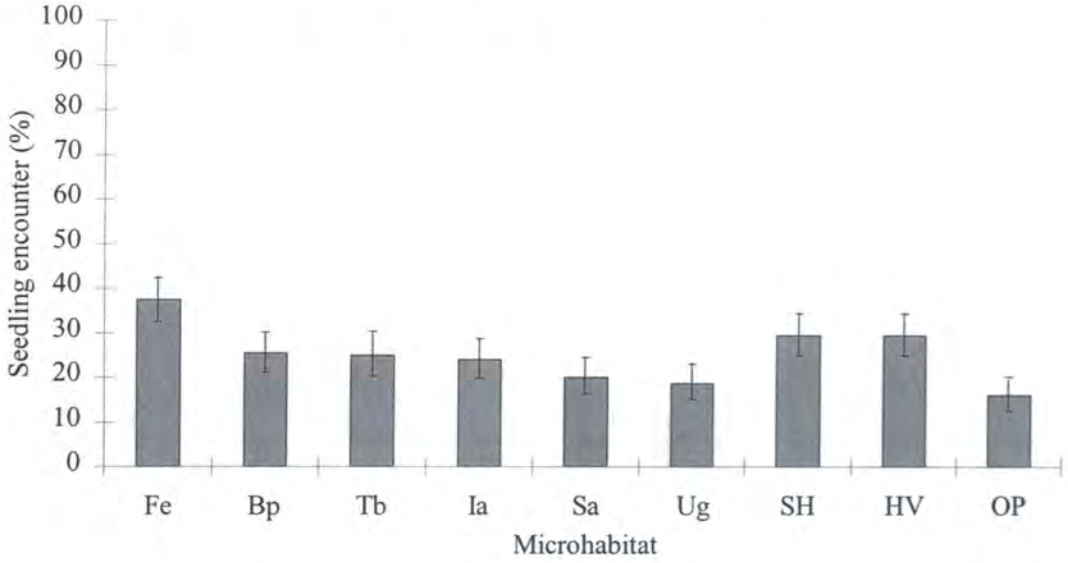
Source	df	SS	MS	F	p
Species (sp)	4	98.15	24.538	30.531	✶✶✶
Microhabitat (mh)	8	16.16	2.02	2.513	✶
Treatment (tr)	2	49.42	24.710	30.746	✶✶✶
Sp.mh	31	44.99	1.451	1.806	✶✶
Sp.tr	8	19.94	2.493	3.101	✶✶
Mh.tr	16	20.15	1.259	1.567	n.s.
Sp.mh.tr	62	69.14	1.115	1.388	n.s.
Residual	528	424.35	0.8037		
Total	659	742.28			

Figure 5.2. Mean percentage seedling encounter (± 1 S.E.) for each species, at each treatment.



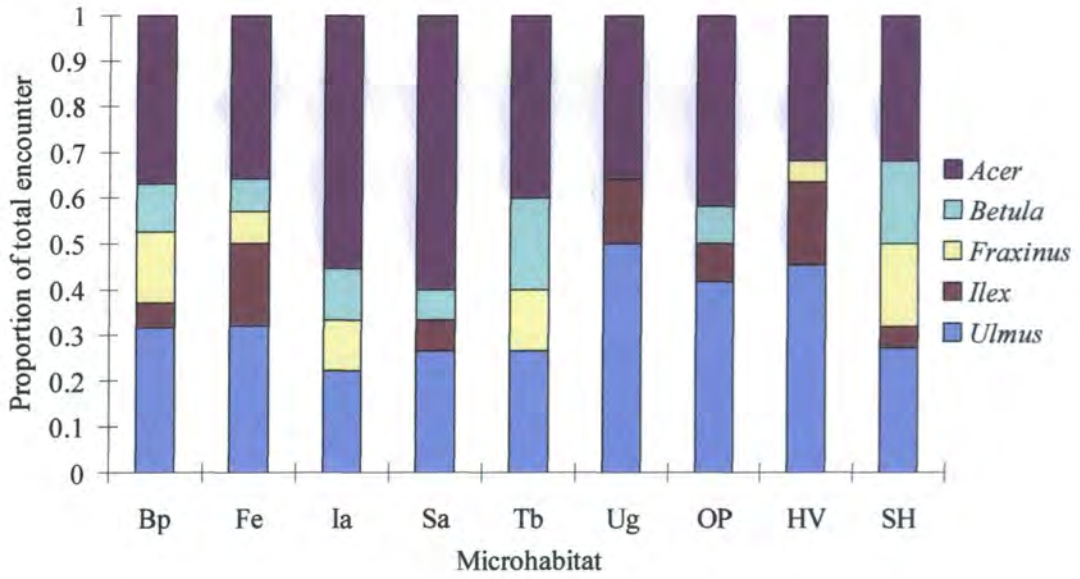
Rates of seedling encounter varied significantly between microhabitats (Table 5.3, Figure 5.3). Encounter was significantly greater beneath adults of *Fraxinus* than beneath adults of other taxa, and was significantly lower in Open microhabitats than beneath Shrub and High Vegetation, where rates of encounter were similar. Variation between microhabitats was similar between treatments (Table 5.3).

Figure 5.3. Mean percentage seedling encounter (± 1 S.E.) for each microhabitat (*Betula* [Bp], *Fraxinus* [Fe], *Ilex* [Ia], *Sorbus* [Sa], *Taxus* [Tb], *Ulmus* [Ug], Shrub [SH], High vegetation [HV] and Open [OP]).



Variation between species was also microhabitat dependent (Table 5.3, Figure 5.4). In the majority of microhabitats, seedlings of *Acer* were more frequently encountered than seedlings of any other taxon. Beneath *Ulmus* and High Vegetation, *Ulmus* seedlings were most encountered and in Open microhabitats, *Acer* and *Ulmus* seedlings were encountered at similar rates. Only beneath adults of *Ulmus* were conspecific seedlings encountered more frequently than seedlings of any other taxon. Beneath *Ilex*, conspecific seedlings were encountered less frequently than any other taxon. There was no interaction between species, microhabitat and treatment (Table 5.3).

Figure 5.4. Encounter of each species as a proportion of total seedling encounter in each microhabitat.



5.3.2 **Seedling damage**

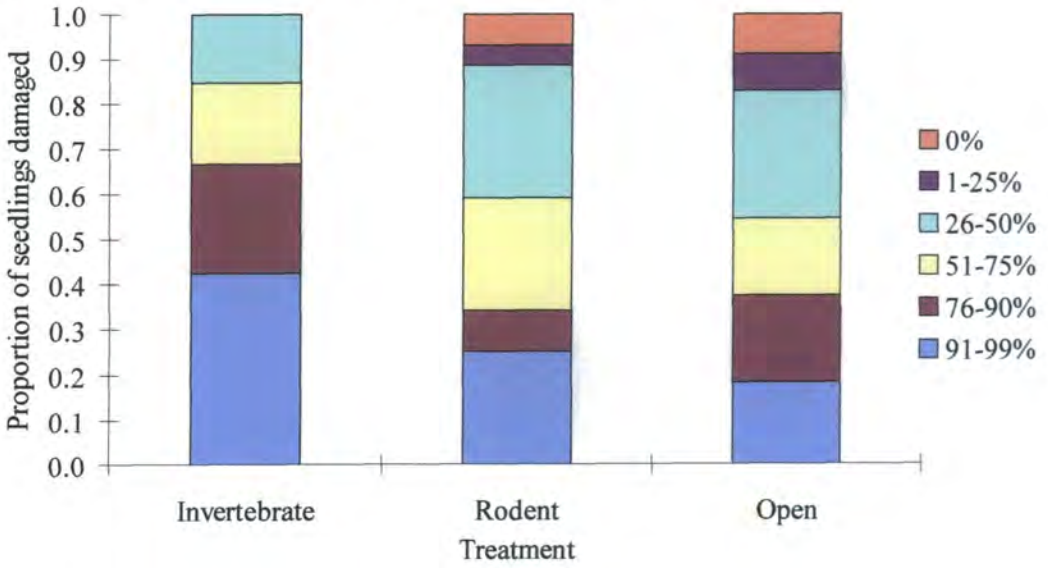
The severity of seedling damage, once encountered, was similar between microhabitats (χ^2=10.741, df=8, p>0.05) and varied significantly between treatments (χ^2=17.133, df=8, p<0.05, Figure 5.5). This variation was principally between Invertebrate and the other treatments, since patterns of seedling damage at Rodent and Open depots were similar (χ^2=4.233, df=5, p>0.05). The majority of invertebrate damage was of minor severity, having a low modal damage category (91-99% remaining), and no seedling damage occurred at the highest damage categories (0-25% remaining). Sixty-seven percent of invertebrate damaged seedlings had more than seventy-five percent of their tissue remaining after herbivory.

At Rodent and Open depots, a greater proportion of seedlings was subject to high category damage, with eleven and seventeen percent of seedlings, respectively, either completely consumed or less than 25 % intact. Both treatments had high modal damage categories (26-50% remaining) and relative to invertebrate damage, fewer seedlings were subject to minor damage. At Rodent and Open depots, less than thirty-five and forty percent of seedlings, respectively, had more than seventy-five percent of their tissue remaining after herbivory.

There was no spatial association between levels of seedling damage at Invertebrate and Rodent treatments (r_S=0.225, df=7, p>0.05), Invertebrate and Open

treatments (r_S=0.128, df=20, p>0.05) or Rodent and Open treatments (r_S=0.222, df=24, p>0.05).

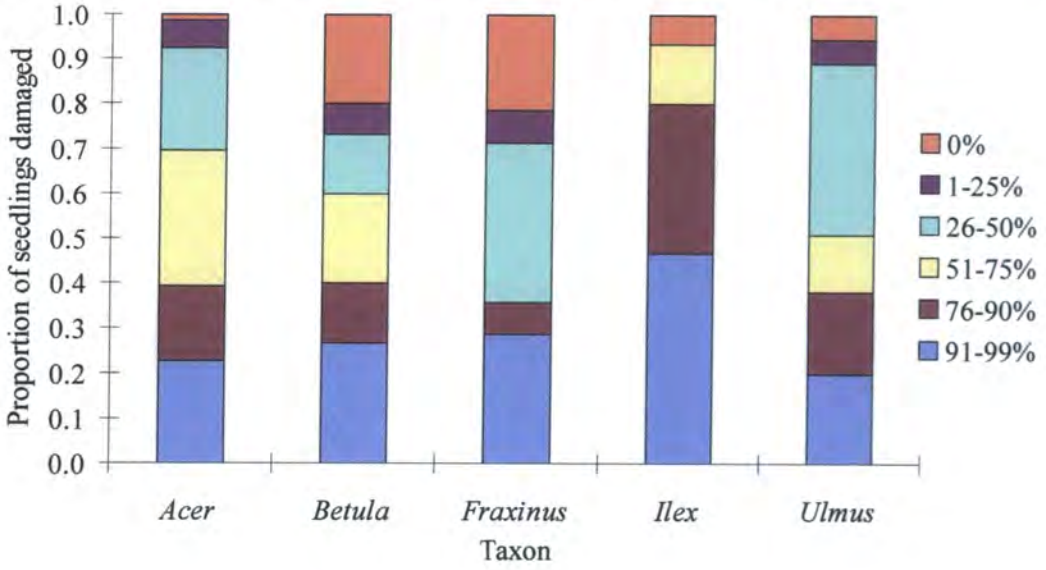
Figure 5.5. Proportion of total seedling damage within categories reflecting the percentage of seedling remaining after herbivory, for each treatment.



The severity of seedling damage, once encountered, varied significantly between tree species (χ^2=17.133, df=8, p<0.05, Figure 5.6). In fact, patterns of seedling damage were similar for *Acer*, *Betula*, *Fraxinus* and *Ulmus* (χ^2=8.175, df=6, p>0.05). *Ilex* was distinct in the frequency of low category seedling damage, with eighty percent of damaged seedlings having more than seventy-five percent of their tissue remaining after herbivory. Once encountered, seedlings of other species were more likely subject to higher category seedling damage (0-75% remaining).

Data were insufficient to investigate the significance of higher order interactions between treatment, species and microhabitat. The conditions of chi-squared analysis, regarding the lower limit of expected frequencies, could not be fulfilled even after pooling damage categories.

Figure 5.6. Proportion of total seedling damage within categories reflecting the percentage of seedling remaining after herbivory, for each tree species.



5.3.3 **Variation with respect to seedling characteristics**

Rates of seedling encounter and damage at Invertebrate, Rodent and Open depots were not significantly associated with any of the growth, allocation or leaf parameters measured (Tables 5.4 and 5.5). Although the median severity of seedling damage at Open depots was correlated with the leaf plus cotyledon mass fraction and mean relative growth rate of seedlings, such associations were likely to be unreliable since marginal significance was lost with the omission of outlying data (*Ilex* seedling damage). Total seedling mass, leaf plus cotyledon mass, saturated leaf mass:dry leaf mass ratio, leaf plus cotyledon mass fraction and mean relative growth rate were, therefore, poor predictors of seedling encounter and damage.

Table 5.4. Characteristics of tree seedlings of each study species; total seedling dry mass (mg dm/sdlg, mg dry mass per seedling), total leaf plus cotyledon (L+C) dry mass, saturated leaf (SL) mass:dry leaf (DL) mass ratio, leaf plus cotyledon mass fraction and mean relative growth rate (RGR)(ss d^{-1}, growth rate per day, excluding cotyledons). All parameters were taken or calculated from values in Cornelissen *et al.* (1996).

Taxon	Total mass (mg dm/sdlg)	L+C mass (mg dm/sdlg)	SL mass/ DL mass	L+C mass fraction	Mean RGR ss (d^{-1})
Acer	44.3	24.7	3.63	0.558	0.081
Betula	0.6	0.4	3.57	0.719	0.128
Fraxinus	25.3	14.3	3.98	0.566	0.102
Ilex	12.1	4.8	3.87	0.401	0.014
Ulmus	2.9	1.8	3.61	0.621	0.12

Table 5.5. Results of Pearson sample correlations between seedling characteristics and the proportion of seedlings encountered and Spearman rank correlations between seedling characteristics and the median severity of seedling damage. Pearson (r) and Spearman (r_s) correlation coefficients and degrees of freedom (df) are included for each treatment. Significance levels (p) included; ≥0.05, (n.s., not significant) and <0.05 (✶).

	Invertebrate			Rodent			Open		
Encounter	r	df	*p*	r	df	*p*	r	df	*p*
Total mass	0.526	3	n.s.	0.317	3	n.s.	0.435	3	n.s.
L+C mass	0.550	3	n.s.	0.318	3	n.s.	0.469	3	n.s.
SL mass/DL mass	-0.649	3	n.s.	-0.574	3	n.s.	-0.437	3	n.s.
L+C mass fraction	0.169	3	n.s.	-0.095	3	n.s.	0.102	3	n.s.
Mean RGR	0.169	3	n.s.	-0.069	3	n.s.	0.243	3	n.s.
Damage	r_s	df	*p*	r_s	df	*p*	r_s	df	*p*
Total mass	0.053	3	n.s.	-0.564	3	n.s.	-0.447	3	n.s.
L+C mass	0.053	3	n.s.	-0.564	3	n.s.	-0.447	3	n.s.
SL mass/DL mass	-0.527	3	n.s.	-0.872	3	n.s.	-0.335	3	n.s.
L+C mass fraction	0.000	3	n.s.	0.718	3	n.s.	0.894	3	✶
Mean RGR	0.000	3	n.s.	0.718	3	n.s.	0.894	3	✶

5.4 DISCUSSION

5.4.1 **Impact of predator groups**

Rates of invertebrate seedling encounter were low (15.0%, Figure 5.2) and once encountered, the majority of seedlings were subject to relatively light seedling damage (Figure 5.5). Rodent seedling encounter was also relatively low (20.0%, Figure 5.2), although once encountered, a greater proportion of seedlings were subject to high level damage (Figure 5.5). Although rates of encounter were similar, patterns of encounter and damage at Invertebrate and Rodent treatments were not spatially correlated. Variation between species was broadly similar between Invertebrate and Rodent treatments (consistent with Hulme (1994b) in grassland), with the exception of *Ilex* seedlings that were infrequently encountered by invertebrates (Figure 5.2).

At Open depots, rates of seedling encounter were twice the magnitude of the other treatments (40.0%, Figure 5.2) and once encountered, a high proportion of seedlings were severely damaged (<25% remaining, Figure 5.5). Rates of seedling encounter at Open depots were spatially correlated with rates of encounter at Invertebrate and Rodent depots. The encounter of *Acer*, *Ulmus* and *Fraxinus* seedlings at Open depots was proportionally greater than at Invertebrate and Rodent depots (Figure 5.2).

Consistent with studies of tree seedling survival in temperate deciduous woodland (Table 5.1), seedling damage was attributable to a mixed suite of seedling herbivores. Patterns of rodent and invertebrate encounter were similar, although the characteristics of seedling damage were distinct (Hulme, 1994b). High rates of *Fraxinus* seedling encounter at Open depots were not accounted for by invertebrate or rodent herbivory and were likely to reflect the activity of an additional herbivore group. Deer and rabbits were frequently observed foraging on the forest floor and were the most likely alternative seedling herbivores (Wood, 1938; Peterken, 1966; Rousi *et al.*, 1996; Akashi, 1997).

Comparable investigations of tree seedling herbivory (Table 5.1) support the observation that seedling damage characteristics were distinctive between herbivore groups. Molluscs have been typically found to graze cotyledons and, less frequently, primary leaves and growing points, leaving the vascular system largely intact (Southwood *et al.*, 1988; Humphrey & Swaine, 1997b). In contrast, lepidopteran larvae take large chunks from leaves, leaving only a portion of the midrib (Humphrey

& Swaine, 1997b). Molluscs, lepidopteran larvae and beetles also kill seedlings by severing their hypocotyl and radicle (Watt, 1923; Southwood *et al.*, 1988). Although seedlings may be totally defoliated by insects, leaf damage is more often slight, with only a small part of the leaf consumed (Wood, 1938). Beetle larvae also consume tap roots, often resulting in seedling death (Wood, 1938).

Rodents consume cotyledons and sever seedlings at or below the hypocotyl, and in experiments with captive bank voles (*Clethrionomys glareolus*), the pattern of damage to small saplings was characteristic of each tree species (Pigott, 1985). Rodent attack often closely resembles that of invertebrates, although removal of the pericarp and radicle was more characteristic of rodent damage (Watt, 1923). Shoots severed by rodents are often cut into short lengths or left intact on the soil (Watt, 1919; Pigott, 1985). In contrast, rabbits and deer typically tear off cotyledons and primary leaves or sever seedlings close to the ground, consuming them in their entirety (Watt, 1919; Watt, 1923; Rousi *et al.*, 1996; Akashi, 1997). In the present study, the light grazing of seedlings at Open depots was most likely attributable to invertebrate and rodent herbivory.

5.4.2 **Variation between species**

At Invertebrate, Rodent and Open treatments, seedlings of *Acer* and *Ulmus* were more frequently encountered than seedlings of *Ilex*, *Betula* and *Fraxinus* (Figure 5.2). The encounter of *Acer*, *Ulmus* and *Fraxinus* seedlings was proportionally higher at Open treatments, the encounter of *Ilex* seedlings was proportionally lower at Invertebrate treatments and seedlings of *Betula* were infrequently encountered (<20%) at all treatments. Once encountered, seedlings of *Ilex* were subject to a significantly lower intensity of damage than seedlings of other taxa (Figure 5.6).

Seedling herbivores were clearly making selective, rather than random, foraging decisions. Field studies of tree seedling herbivory in temperate deciduous woodland (Table 5.1) support the extensive herbivory of *Acer* and *Ulmus*, the moderate herbivory of *Fraxinus* and the infrequent herbivory of *Betula* seedlings (Sviridenko, 1940, cited in Golley *et al.*, 1975; Rotschild & Krivosheyev, 1957, cited in Pigott, 1985; Wardle, 1959; Linhart & Whelan, 1980; Pigott, 1985). Pigott (1985) also found that six to twenty-one month old saplings of *Acer* were significantly more susceptible to herbivory by captive bank voles (*Clethrionomys glareolus*), than saplings of *Fraxinus* and *Betula*.

In an investigation of *Acer* seedling mortality in mixed deciduous woodland, Paterson *et al.* (1996) found that molluscs were responsible for ninety per cent of seedling deaths, while rodents were of minor importance. In the present study, however, invertebrates and rodents encountered a similar proportion of *Acer* seedlings (40.0 and 37.8%, respectively) and once encountered, rodents damaged seedlings to a greater extent than invertebrates (median damage categories 26-50% and 1-25% remaining, respectively). Although low rates of *Ilex* seedling encounter and damage were recorded in the present study, Peterken (1966) found that seedlings of *Ilex* were abundant in a woodland enclosure from which roe and fallow deer were excluded, but were absent from a similar, adjacent enclosure containing deer.

In a study of seedling herbivory in grassland, Hulme (1994b) found that both molluscs and rodents encountered species with small seedlings (≤1mg dry mass) less frequently than species with large seedlings. Although more frequently encountered by molluscs, large seedlings were damaged to a lesser extent than smaller seedlings. Seedlings which were most frequently encountered by rodents were also most severely damaged. These feeding patterns were thought to reflect the coincidence of cyanogenic ability and large seedling size, and differences in the susceptibility of molluscs and rodents to cyanogenesis.

A number of studies have found that species of seedling with high resistance to mammalian herbivory contain high concentrations of defensive secondary compounds (phenolics, papyriferic acid and related low molecular weight terpenoids) and have much higher phenotypic plasticity than low resistance species (Helle *et al.*, 1986; Tahvanainen *et al.*, 1991; Taipale *et al.*, 1994 – all cited in Rousi *et al.*, 1996; Reichardt *et al.*, 1984). Avoidance of seedling damage may also occur temporally, if germination is delayed to coincide with a period of low herbivore activity (Wood, 1938).

In an investigation of optimal foraging by snowshoe hares (*Lepus americanus*), Schmitz *et al.* (1992) found that the selection of food items was not based exclusively on the maximisation of nutrient intake (including protein and energy) or the avoidance of toxic secondary compounds. Rather, dietary preferences were dependent on the relative chemical and physical attributes of available browse

species. Foraging decisions by rodent seed predators have been found to have a similar basis (Chapter 3).

Jennings & Barkham (1975) support the selective feeding habits of molluscs. The consumption of fresh plant leaves was influenced by the presence of epidermal hairs, and only those glabrous leaves with a soft epidermis were consumed. Leaves with hard exteriors were largely unpalatable, although the largest species studied, *Arion ater*, was less selective. Robertson (1991) also found that leaf chemistry and toughness significantly influenced the severity of leaf damage by insect herbivores. In the present study, low rates of *Ilex* seedling encounter and damage by invertebrates may reflect the low palatability of leathery and waxy leaves.

Wittich (1953, cited in Jennings & Barkham, 1975) found that leaves of *Acer* and *Ulmus* had a high protein content, which may have contributed to their high palatability. Alternatively, apparent preference for protein-rich foods may have resulted from the coincidence of high nitrogen and high sugar content, to which molluscs were found to be sensitive. Jennings & Barkham (1975) also reported the total consumption of individual seedlings of *Acer, Fraxinus* and *Ulmus* by molluscs. In the present study, molluscs encountered no seedlings of *Fraxinus* and seedlings of other taxa were only partially damaged.

In the present study, rates of seedling encounter and damage at Invertebrate, Rodent and Open depots were not significantly associated with any one of the physical attributes measured (total seedling mass, leaf plus cotyledon mass, saturated leaf mass:dry leaf mass ratio, leaf plus cotyledon mass fraction and mean relative growth rate; Tables 5.4 and 5.5). High rates of *Acer* and *Ulmus* seedling encounter and low rates of *Betula* seedling encounter were consistent between herbivore groups. In contrast, the encounter of *Ilex* seedlings by invertebrates was proportionally lower than that of the other herbivore groups, and the encounter of *Fraxinus* seedlings by large mammals proportionally higher. Herbivore groups were making unique foraging decisions, although the parameters that determined rates of seedling encounter and damage were not easily distinguished.

For the majority of species, preferences were most likely individualistic, trade-off responses (Schmitz *et al.*, 1992) to physical (seedling size, Hulme, 1994b; leaf toughness, Jennings & Barkham, 1975; Robertson, 1991) and chemical (nutritional value and toxicity, Rousi, 1996; Reichardt *et al.*, 1984) seedling attributes, according

to dietary requirements and tolerance of plant defence mechanisms. Seedling preferences may have also been confounded by temporal variation in the availability of vegetation cover and alternative food resources, and the population density of seedling herbivores at the time of seedling presentation.

5.4.3 **Variation between microhabitats**

Rates of seedling encounter varied significantly between microhabitats (Figure 5.3). Rather than foraging randomly, seedling herbivores made selective decisions regarding habitat suitability. Seedling encounter was significantly greater beneath adult trees of *Fraxinus* than beneath adults of other tree taxa, and was significantly lower in Open microhabitats than beneath Shrub and High Vegetation. Once encountered, however, the intensity of seedling damage was similar between microhabitats. Greater survival of seedlings in open microhabitats was consistent with the findings of Bramble & Goddard (1942) and Peterken (1966) and followed patterns of seed predation (Chapter 3), reflecting the reduced foraging activity of seedling herbivores. Preferential foraging beneath protective vegetation cover has been observed for both molluscs and rodents (Elton, 1942; Price, 1978; Godan, 1983), although the criteria for optimum cover are likely to differ between groups. In contrast, Morgan (1991) found that scrub understorey provided a nursery for shade tolerant seedlings until branches were sufficiently high to escape browsing animals. Similar recruitment of *Quercus*, *Taxus* and other hardwood trees has been observed beneath the spiny branches of *Crataegus monogyna, Ilex aquifolium* and *Prunus spinosa* (Watt, 1919; Peterken & Tubbs, 1965; Hulme, 1996a).

The availability of vegetation cover may also account for preferential foraging beneath adult trees of *Fraxinus*, although plant associations and the extent of field layer and canopy vegetation cover beneath adults of each taxon were not quantified. The density of molluscs beneath adult trees may also vary between tree species according to the depth of conspecific leaf litter (Paterson *et al.*, 1996). The encounter of *Fraxinus* seeds by rodents was positively density-dependent following abundant fruit production in 1997 (Chapter 4). Increased rodent activity beneath fruiting adults of *Fraxinus* may have accounted for proportionally higher rates of seedling encounter. This was unlikely, however, as seeds of *Fraxinus* were of low preference to rodents (Chapter 3), no significant distance response was observed within fifteen metres of conspecific adult trees (Chapter 4), rodents were satiated by high densities of

Fraxinus seed at a population level and rodents were not the most important seedling herbivores. Although rates of seedling encounter were significantly greater beneath adults of *Fraxinus* than beneath adults of other taxa, the characteristics that determined habitat suitability were not easily distinguished.

Humphrey & Swaine (1997b) recorded greater herbivory of *Quercus* spp. seedlings beneath a conspecific canopy than beneath *Betula* spp. Similarly, Maeto & Fukuyama (1997) found that *Acer* seedling mortality was greater beneath canopies containing conspecific adults than beneath canopies from which they were absent. These patterns reflected some degree of host specificity, with insects defoliating the canopy and falling beneath adults to consume seedlings. Paterson *et al.* (1996) also recorded greater herbivory of *Acer pseudoplatanus* seedlings beneath conspecific adults, where the thick leaf litter provided an ideal habitat for molluscs (Philipson, 1983). In the present study, seedlings of *Ulmus* were more frequently encountered beneath conspecific adults than beneath adults of other tree taxa. This may have occurred as a chance effect, however, and there was no overall trend that rates of seedling encounter were greater beneath conspecific adults. An absence of host-specificity would have also been consistent with observed patterns of seed predation (Chapter 3), more likely reflecting opportunistic foraging by generalist seedling herbivores.

5.4.4 **Seedling growth and survival**

Although herbivore damage may not have resulted in the mortality of seedlings, which have a limited potential for recovery, the probability of survival was likely to have declined with increasing damage. Pigott (1985) found that the only tree seedlings (<20cm high, without cotyledons) that failed to recover from herbivory, were those that had been severed at the hypocotyl. The younger seedlings presented in the present study (<1 month old, with cotyledons and first true leaves) were likely to have been more sensitive to herbivory, during the early stages of growth and establishment. Seedlings were more likely to have recovered from light invertebrate damage than more severe damage inflicted by mammalian herbivores. There is also some evidence that large seed size may be an advantage to herbivore tolerance through resprouting (Harms & Dalling, 1997), although seedlings which do survive herbivory may be limited in growth and competitive ability (Hendrix, 1988). In

addition, defoliation may delay leafing time and alter carbohydrate relations in the roots (Raitio *et al.*, 1994).

5.4.5 **Impact of seedling herbivory on plant demography**

Mammals encountered seedlings more frequently than invertebrates, and once encountered, inflicted a greater severity of damage, for which seedlings had a lower probability of recovery. Mammals were, therefore, likely to have had a greater impact on plant regeneration than invertebrates. Although seedling herbivores foraged broadly across all microhabitats, proportionally lower seedling encounter in the open may have influenced spatial patterns of recruitment. In addition, variation between plant species may have been significant to community composition. Ultimately, the impact of seedling herbivory on plant recruitment is likely to depend on the natural density of seedlings, the environmental requirements of seedling establishment and plant survival (Callaway, 1992; Herrera *et al.*, 1994; Hulme, 1996a) and the magnitude of alternative biotic and abiotic mortality factors (Bramble & Goddard, 1942; Augspurger, 1984; Goldberg, 1985; Streng *et al.*, 1989; Gill & Marks, 1991; Reader, 1993; Jones *et al.*, 1994).

CHAPTER 6

NATURAL SEEDLING DYNAMICS

6.1 INTRODUCTION

6.1.1 **Studies of seedling recruitment**

Woodland regeneration is critically dependent on the successful recruitment of tree seedlings, although patterns of seedling demography may be highly variable in both time and space (Watt, 1919, 1923; Shaw, 1968 a, b; Linhart & Whelan, 1980; Hulme, 1996a). Studies of the regenerative phase of temperate deciduous woodland have principally considered the post-dispersal survival and germination of tree seeds and the establishment, growth and survival of tree seedlings. Spatial and temporal patterns of seedling recruitment were typically non-random (Linhart & Whelan, 1980; Morgan 1991) and often varied significantly between tree species (Pigott, 1983; Evans, 1988; Harmer *et al.*, 1997).

Although seed and seedling predation have been identified as principal components of the regeneration environment (Chapters 3, 4, 5), seed germination and seedling development and survival may be significantly influenced by alternative biotic and abiotic factors. A complexity of such factors may ultimately determine the abundance and spatial distribution of seedling recruitment, and potentially limit the natural regeneration of temperate deciduous woodland.

6.1.2 **Seed germination**

Tree seeds are particularly vulnerable to critical water loss, which may be sufficient to limit germination. Rapid desiccation to a lethal level may follow exposure on a dry soil surface to an atmosphere of low relative humidity and rainfall (Watt, 1919, 1923; Shaw, 1968b). The cover provided by soil, leaf litter, branches, moss, shrubs and ferns has been found to increase rates of germination by depressing water loss from the seed (Watt, 1919, 1923; Wood, 1938; Shaw, 1968b; Pigott, 1983). At the same time, such cover may limit the germination of light-demanding species, such as *Betula pendula* (Watt, 1919; Pigott, 1983; Goldberg, 1985) and may be impenetrable to emerging seedlings with insufficient resources. Dense vegetation cover may support seeds and prevent them from reaching the soil, leading to exposure to desiccation (Watt, 1919). Conversely, burial at greater depths beneath compact soil and litter layers may prevent penetration to the surface (Watt, 1923, Wood, 1938).

Direct access to liquid water was found to be essential for the germination of *Fagus sylvatica* (Watt, 1923) and *Quercus petraea* (Shaw, 1968b). A film of water in contact with the seed was necessary to maintain the level of water uptake above the level of water loss for long enough to induce germination. The absence of a film of water was not compensated for by high relative humidity, although this was advantageous in reducing desiccation. Full immersion in acidic, poorly oxygenated, waterlogged soil, however, dramatically reduced seed germination and survival, and subsequently increased the exposure of seedlings to fungal disease (Tapper, 1992).

Tapper (1992) found that an unusually cold winter followed by late snow melt and a cold and wet spring, was sufficient to reduce the germination of *Fraxinus excelsior* to six per cent of that expected. Wood (1938) recorded greater stability of soil surface temperature beneath leaf litter, which may account for the higher rates of germination recorded. Canopy cover may also favour tree seed germination by providing protection from extremes of wind, precipitation and sunlight, as well supplying a protective covering of leaves (Wood, 1938; Goldberg,1985).

The germination of *Ilex aquifolium*, as indicated by emergence above ground, was found to be greatest beneath conspecific adult trees, reflecting the inefficiency of seed dispersal (Peterken, 1966). Melzack & Watts (1982) found that seeds of *Taxus baccata* often germinated beneath a scrub cover of *Crataegus monogyna* or *Juniperus communis*. This would support evidence that the regeneration of *T. baccata* was dependent on the availability of such microsites (Hulme, 1996a).

6.1.3 **Seedling growth and development**

Vegetation cover may also influence the biomass, morphology and physiology of seedlings as a result of the interception of light and precipitation, and the removal of moisture and nutrients from the soil. Seedling growth may be significantly reduced or completely restricted beneath dense field layer (Watt, 1923; Peterken, 1966; Tapper, 1992) or canopy cover (Pigott, 1983; Emborg, 1998). Smothering by the dying fronds of *Pteridium aquilinum* (Humphrey & Swaine, 1997a), excessive soil acidity or alkalinity (Wood, 1938) and the lack of appropriate mycorrhizal associates (Goldberg, 1985), have also been found to locally restrict seedling growth and development.

Low relative light intensity may also decrease seedling vigour (Peterken, 1966), increase specific leaf area and leaf area ratios, and decrease root:shoot ratios

(Humphrey & Swaine, 1997a). Lei & Lechowicz (1998) recorded the complex physiological responses of tree seedlings to woodland gap formation. Increased light intensity resulted in greater stomatal conductance, chlorophyll a:b ratios, leaf nitrogen concentrations and maximum photosynthetic rates, and lower leaf internal carbon-dioxide concentrations. It is significant that seedlings which are suppressed by low light intensity are less resistant towards additional deleterious factors, such as drought and fungal disease, which may coact to further limit seedling growth and survival (Watt, 1919, 1923; Peterken, 1966). Interspecific competition between seedlings at high density, particularly beneath shade, may also result in etiolated growth (Evans, 1988) and high rates of mortality (Taylor & Aarssen, 1989; Tapper, 1992; Nakashizuka *et al.*, 1995).

6.1.4 **Seedling establishment and survival**

Light stress may directly inhibit the survival of light-demanding species beneath dense field layer (Linhart & Whelan, 1980; Evans, 1988) or canopy cover (Peterken, 1966; Pigott, 1983; Boerner & Brinkman, 1996), such that successful regeneration would depend on partial or full removal of the field layer (Goldberg, 1985; Tapper, 1992) or the opening of the canopy (Morgan, 1991). Marquis *et al.* (1975, cited in Harmer *et al.*, 1997) found that the natural regeneration of hardwood stands in the USA was unlikely where the cover of grasses, sedges and pteridophytes exceeded thirty per cent. Additional mortality factors associated with vegetation cover, include the removal of moisture and nutrients from the soil (Evans, 1988), the accumulation of leaf litter (Peterken, 1966; Linhart & Whelan, 1980) and the smothering and toxic action of decaying plant material overlying seedlings (Watt, 1919). Field layer cover may also harbour rodent seed and seedling predators (Chapters 3 & 5), whereas scrub understorey may protect seedlings from larger herbivores (Morgan, 1991).

Seedling establishment and survival may be greater beneath dense canopy cover if the vigour and abundance of herb growth is negatively associated with the extent of the canopy (Harmer *et al.*, 1997). Wardle (1959) found that the survival of *F. excelsior* seedlings was greater beneath the closed canopy of *F. sylvatica* than beneath the open canopy of *F. excelsior*, since the former shaded out a dense layer of *Mercurialis perennis* which would otherwise limit seedling recruitment (Wardle, 1959). Watt (1923) also observed that the increased density of ungrazed shrub and

herbaceous vegetation following canopy gap formation was sufficient to exclude seedlings of *F. sylvatica* unless partially suppressed. The fronds of *P. aquilinum* may also shade the soil sufficiently to reduce the growth of herbs and prevent soil desiccation, supporting the regeneration of *I. aquilinum* seedlings which are able to withstand the conditions of shade and smothering (Peterken, 1966). Similarly, species including *F. excelsior* may regenerate successfully on relatively poor, dry and unstable soils, if such conditions favour seedlings over the field layer (Wardle, 1959, 1961; Harmer *et al.*, 1997).

Canopy cover may also increase seedling survival by ameliorating extremes of temperature, although seedling growth and development is compromised by low light intensity (Wood, 1938). Evans (1988) proposed optimal semi-shade conditions for the natural regeneration of broadleaves, where intermediate levels of light, moisture and leaf litter would favour seedling germination and establishment while suppressing vigorous herb growth, fungal attack and frost damage. Preference for semi-shade conditions was supported by Peltier *et al.* (1997), recording the germination and establishment of *F.sylvatica* and *F.excelsior* seedlings. Low recruitment in canopy gaps was also attributed to poor soil conditions.

Seedling establishment and survival may be either positively (Houle, 1995; Clark *et al.*, 1998) or negatively (Nakashizuka *et al.*, 1995) associated with spatial patterns of seed rain, often reflecting the density and location of the source. Seed crop size may also account for annual variation in seedling recruitment (Tapper, 1992), with peaks in seedling density often following mast seeding (Shaw, 1968a; Evans, 1988; Boerner & Brinkman, 1996). Goldberg (1985), however, found no association between the recruitment of *Quercus albocincta* seedlings and the abundant production of seeds. Nakashizuka *et al.* (1995) recorded a negative association between seedling survival and the number of seeds produced per fruiting individual, reflecting a strong negative correlation between seed crop size and seed size, and a positive correlation between seed size and seedling survival. Seed production may also account for variation in regeneration between sites. In natural woodlands of *T. baccata*, Hulme (1994c) recorded the greatest density of seedlings at the site with the highest production of seed, although overall recruitment per tree differed little between sites.

The response of seedlings to environmental factors was often age dependent. Peterken (1966) observed that younger seedlings had greater mortality rates than older

seedlings. Rather than being subject to a greater variety of mortality factors, young seedlings were subject to greater intensities of the same factors. For example, young seedlings may be more susceptible to damping-off disease (Tapper, 1992) and drought stress (Peterken, 1966), as a result of being more shallow rooted.

Seedling responses to limiting factors may also vary significantly between tree species. Pigott (1983) recorded the rapid mortality of *B. pendula* seedlings beneath the dense canopy of *Acer pseudoplatanus*. Seedlings of *Q. petraea* and *Sorbus aucuparia* survived to the following year, although only seedlings of *S. aucuparia* increased significantly in biomass. The development of canopy and field layer cover may, consequently, result in a succession of recruitment as conditions favour or disadvantage alternative species. Evans (1988) observed that an increase in canopy cover was sufficient to eliminate *B. pendula* and favour the regeneration of *A. pseudoplatanus* over *F. excelsior*, while having little effect on the recruitment of *F. sylvatica*. Linhart & Whelan (1980) also recorded the replacement of light-demanding species by shade tolerant species, following an increase in field layer cover. Variable tolerances to environmental factors may also influence the germination behaviour of tree species, with a potential trade-off between late germination to avoid frost damage (Evans, 1988) and early germination to precede summer drought (Hett & Loucks, 1971) and the maximum cover of the field layer (Tapper, 1992). Overall, the intensity of limiting factors and the rates of seedling mortality are most likely greater in the summer than in the winter (Tapper, 1992).

6.1.5 **Study aims**

Although the complexity of biotic and abiotic factors influencing spatial and temporal patterns of seedling recruitment have been recognised, few studies have investigated the combined effect of such factors (Morgan, 1991; Peltier *et al.*, 1997). To address this, the present study adopts a multivariate approach to investigate the relationships between habitat characteristics and seedling demographic patterns, which may contribute to natural regeneration processes in temperate deciduous woodland.

The specific aims of the study were to:

1. Quantify the spatial and temporal distribution patterns of seedling establishment and survival, forest architecture and ground layer cover in temperate deciduous woodland.
2. Determine whether the natural abundance, survivorship and spatial distribution of seedlings varied significantly between tree species and seedling cohorts.
3. Examine the relationships between seedling recruitment and habitat characteristics.

6.2 METHODS

6.2.1 **Seedling surveys**

The dynamics of natural seedling abundance were monitored in Shipley Wood, where patterns of seedling herbivory had been quantified in a concurrent investigation (Chapter 5). The study area was surveyed systematically using three equidistant linear transects traversing upper, middle and lower regions of the site (Figure 2.2), each with fifteen 1m x 1m permanent quadrats (Jones *et al.*, 1994; Nakashizuka *et al.*, 1995) at twenty metre intervals. Surveys were conducted at intervals of twenty-eight to forty days between 9th May 1996 and 9th December 1997. During each survey, the number of seedlings of each study species within each quadrat, was recorded. Seedling taxa included *Acer*, *Betula*, *Fraxinus*, *Ilex*, *Sorbus*, *Taxus* and *Ulmus*. In addition, the percentage cover of leaf litter, bare ground and the principal ground vegetation components (broad-leaved herbs, ferns, graminoids, shrub and moss) were estimated using the domin scale (Dahl & Hadac, 1941, cited in Rodwell, 1991). All seedlings were marked using tape flags attatched to the hypocotyl (Herrera *et al.*, 1994; Jones *et al.*, 1994). Unique colour markings were used to distinguish "Persistent" seedlings, recorded at the beginning of the survey after at least one year of survival, and subsequent cohorts of "Germinant" seedlings that emerged during the surveys which followed.

Between 16th April and 9th December 1997, the experimental design was modified to determine the impact of mollusc herbivory on seedling density. Molluscs were eliminated from a randomly selected half of each quadrat using a metaldehyde molluscicide (Shower-proof Bioslug®), applied at a density of approximately 20g m^{-2} and replenished at two week intervals. Surveys of vegetation cover and seedling dynamics continued, as described, until 9th December 1997.

6.2.2 **Habitat and tree species characteristics**

At the end of the survey period, additional habitat parameters were measured. The basal area of adult trees in the vicinity of each quadrat was estimated using the 'point-centred quarter method' (Cottam *et al.*, 1953). In addition, the distance and basal girth of the nearest adult neighbours of *Acer*, *Betula* and *Fraxinus* were measured.

Seed output from each taxon was estimated in 1997, at the time of maximum fruit production; *Betula* (15th August), *Fraxinus* (20th February), *Ilex* (21st October), *Sorbus* (15th August), *Taxus* (3rd October), *Ulmus* (26th May). The number of fruit produced by thirty randomly selected adult trees of each species was estimated and the mean number of fruit per tree calculated. The mean number of seeds contained within multi-seeded fruit of *Ilex* and *Sorbus*, and the strobiles of *Betula*, were determined from ten fruit/strobiles collected from each of ten fruiting adult trees of each taxon. The total viable seed output of each study species in Shipley Wood was calculated as a function of adult tree density (Chapter 2), seed viability (Chapter 3) and mean seed production per tree, based on 1997 estimates.

6.2.3 **Statistical analysis**

A Wilcoxon paired-sample test was used to investigate variation in seedling density between half quadrats with and without the application of molluscicide. Variation between tree species in the number of "Persistent" and "Germinant" seedlings, and the total number of seedlings per quadrat, was investigated using a Kruskall-Wallis test. Variation between years in the number "Germinant" seedlings of each species, was investigated using a Mann-Whitney test, corrected for ties. The association between the density of seedlings of each species and parameters including adult tree density, seed mass (Chapter 3), seedling mass (Chapter 5) and viable seed output, was determined using Pearson sample correlations.

Kaplan-Meier survival analysis was used to determine the median survival time of "Germinant" seedlings of each species. The survival time of each seedling was taken as the time between the first and last recording of the seedling. Seedlings still surviving at the end of the survey period were 'censored' by the analysis and compensated for in calculations of median survival time. Since mortality may have occurred at any time between the last recording of the seedling and the following survey, a period of between twenty-eight and forty days, survival times were likely to underestimate absolute survivorship. The Log Rank test statistic was used to determine the equality of survival distributions between seedlings of each species, each cohort and each year.

The association between seedling density and the observed environmental variables was investigated using the multivariate ordination technique of Canonical Correspondence Analysis (CCA) (Ter Braak, 1988, 1995). Seedling data were

categorised in order to distinguish patterns of abundance and survival between tree species and between seedlings of different ages. At each survey, marked seedlings were distinguished as germinating that survey (New germinants), the previous survey (Last survey), before the previous survey, but within the same season (This season) and prior to that season (Previous season+). For each age category, the number of seedlings of each species per quadrat and the survival of seedlings, as the total proportion surviving since marking, were calculated. Surveys were defined as state variables to examine the association between survey date and the pattern of variation in seedling data. Full descriptions of dependent and independent variables are included in Tables 6.1 and 6.2, respectively.

A Monte Carlo test, with nine hundred and ninety-nine random permutations, was incorporated to determine the statistical significance of the first canonical axis and the overall species-environment association. The significance of individual environmental and state variables was determined by regression with each canonical axes and graphical ordination of biplot scores, represented by vectors in the direction of maximum change. The length of vectors reflected the importance of each environmental variable, and the direction, their association with the ordination axes and patterns of seedling data. The overall association between patterns of seedling data and the principal environmental and state variables, for cohorts of each tree species, was assessed from the species-environment biplot.

Table 6.1. Description of dependent variables used in CCA.

Abbreviation	Taxon	Parameter	Age category
ApNN	*Acer*	Number of seedlings	New germinants
ApNL	*Acer*	Number of seedlings	Last survey
ApNT	*Acer*	Number of seedlings	This season
ApNP	*Acer*	Number of seedlings	Previous season+
ApSL	*Acer*	Survival of seedlings	Last survey
ApST	*Acer*	Survival of seedlings	This season
ApSP	*Acer*	Survival of seedlings	Previous season+
BpNN	*Betula*	Number of seedlings	New germinants
BpNL	*Betula*	Number of seedlings	Last survey
BpNT	*Betula*	Number of seedlings	This season
BpNP	*Betula*	Number of seedlings	Previous season+
BpSL	*Betula*	Survival of seedlings	Last survey
BpST	*Betula*	Survival of seedlings	This season
BpSP	*Betula*	Survival of seedlings	Previous season+
FeNN	*Fraxinus*	Number of seedlings	New germinants
FeNL	*Fraxinus*	Number of seedlings	Last survey
FeNT	*Fraxinus*	Number of seedlings	This season
FeNP	*Fraxinus*	Number of seedlings	Previous season+
FeSL	*Fraxinus*	Survival of seedlings	Last survey
FeST	*Fraxinus*	Survival of seedlings	This season
FeSP	*Fraxinus*	Survival of seedlings	Previous season+

Table 6.2. Description of independent variables used in CCA.

Abbreviation	Description	
S1	Survey 1	May 12th–13th, 1996
S2	Survey 2	June 10th-11th, 1996
S3	Survey 3	July 12th-13th, 1996
S4	Survey 4	August 18th-19th, 1996
S5	Survey 5	September 20th–21st, 1996
S6	Survey 6	October 21st-22nd, 1996
S7	Survey 7	November 23rd-24th, 1996
S8	Survey 8	January 2nd-3rd, 1997
S9	Survey 9	February 10th-11th, 1997
S10	Survey 10	March 17th-18th, 1997
S11	Survey 11	April 20th-21st, 1997
S12	Survey 12	May 22nd-23rd, 1997
S13	Survey 13	June 26th-27th, 1997
S14	Survey 14	July 30th-31st, 1997
S15	Survey 15	September 4th-5th, 1997
S16	Survey 16	October 2nd-3rd, 1997
S17	Survey 17	November 6th-7th, 1997
S18	Survey 18	December 9th-10th, 1997
BLHerb	Percentage cover of broad-leaved herbs	
Fern	Percentage cover of ferns	
Gram	Percentage cover of graminoids	
Litter	Percentage cover of leaf litter	
Shrub	Percentage cover of shrub (principally *Rubus* spp.)	
Moss	Percentage cover of moss	
Bare	Percentage cover of bare ground	
BA	Basal area of adult trees (tree hectare $^{-1}$)	
ApD	Distance to nearest adult neighbour of *Acer* (m)	
ApG	Girth of nearest adult neighbour of *Acer* (cm)	
BpD	Distance to nearest adult neighbour of *Betula* (m)	
BpG	Girth of nearest adult neighbour of *Betula* (cm)	
FeD	Distance to nearest adult neighbour of *Fraxinus* (m)	
FeG	Girth of nearest adult neighbour of *Fraxinus* (cm)	

6.3 RESULTS

6.3.1 **Impact of molluscs**

Total seedling density and the density of seedlings of each study species did not differ significantly between half quadrats with and without the application of molluscicide (Table 6.3). Since molluscicide had no significant impact on seedling density, further analysis will consider whole quadrats over the entire study period.

Table 6.3. Results of Wilcoxon paired-sample tests for variation in seedling density between half quadrats with and without the application of molluscicide. Values include mean seedling density m^{-2}, standard error (s.e.), Wilcoxon Z-statistic and sample size (n). Significance levels (p) were ≥ 0.05 (n.s., not significant).

	Molluscicide		No Molluscicide				
Taxon	mean	s.e.	mean	s.e.	Z statistic	n	p
Acer	0.222	0.114	0.134	0.076	-1.342	45	n.s.
Betula	3.600	0.730	4.222	0.882	-0.519	45	n.s.
Fraxinus	1.200	0.338	1.244	0.476	-0.251	45	n.s.
Sorbus	0.044	0.044	0.000	0.000	-1.000	45	n.s.
Total	5.156	0.884	5.688	1.066	-0.539	45	n.s.

6.3.2 **Natural seedling densities**

The total number of seedlings per quadrat varied significantly between tree species over the survey period (Table 6.4). Seedlings of *Betula* were most frequently encountered, whereas, seedlings of *Ilex*, *Sorbus* and *Taxus* were encountered rarely. No seedlings of *Ulmus* were encountered during the survey period. The number of "Persistent" seedlings and the number of "Germinant" seedlings in 1996 and 1997, also varied significantly between species (Table 6.4). "Germinant" seedlings of *Betula* were most abundant, occurring at densities of up to 28 m^{-2}, although "Persistent" seedlings of this taxon were not encountered. In contrast, the density of "Persistent" *Fraxinus* seedlings was greater than the density of "Germinant" seedlings in both years of the survey. The majority of *Acer* seedlings germinated in 1996, at densities of up to 11 m^{-2}, although mean densities were relatively low.

The densities of "Germinant" *Acer* and *Fraxinus* seedlings were significantly greater in 1996 than in 1997 (Table 6.4; Mann-Whitney test, corrected for ties $Z_{45,45}$=-2.248, p<0.05 and $Z_{45,45}$=-2.222, p<0.05, respectively), whereas, the mean densities of "Germinant" *Betula* and *Sorbus* seedlings were similar between years ($Z_{45,45}$=-0.111, p=n.s. and $Z_{45,45}$=-0.597, p=n.s.).

Variation between tree species in mean "Germinant" (1996 and 1997) and total seedling density was positively correlated with the abundance of viable seeds produced by conspecific adult trees (Table 6.5). When *Betula* was excluded from the analysis as a potential outlier, the associations between viable seed output and mean "Germinant" (1996 and 1997) and total seedling density were maintained (r=0.999, df=3, $p<0.01$; r=0.997, df=3, p<0.01 and r=0.999, df=3, p<0.01, respectively). The production of vast numbers of viable seed accounted for the high density of *Betula* and *Fraxinus* seedlings, relative to the low viable seed output and seedling density of *Ilex*, *Sorbus*, *Taxus* and *Ulmus*. The density of "Persistent" seedlings was not correlated with the production of viable seed. Adult tree density, seed mass and seedling mass were poor predictors of seedling density.

Table 6.4. Mean "Persistent", "Germinant" (1996 and 1997) and Total seedling density m^{-2}, for each study species. Included are standard errors (s.e.), range values and results of Kruskall-Wallis analysis for variation between tree species in the number of seedlings per quadrat. Significance levels (p) were <0.001 (★★★).

	"Persistent"			"Germinant"96			"Germinant"97			Total		
Taxon	mean	s.e.	range	mean	s.e.	range	mean	s.e.	range	mean	s.e.	range
Acer	0.07	0.04	0-1	0.58	0.29	0-11	0.02	0.02	0-1	0.67	0.30	0-11
Betula	0.00			6.07	1.25	0-28	3.89	0.67	0-21	9.96	1.66	0-49
Fraxinus	0.78	0.28	0-10	0.69	0.17	0-6	0.33	0.12	0-4	1.80	0.44	0-14
Ilex	0.00			0.04	0.03	0-1	0.00			0.04	0.03	0-1
Sorbus	0.00			0.07	0.05	0-2	0.02	0.02	0-1	0.09	0.05	0-2
Taxus	0.02	0.02	0-1	0.07	0.05	0-2	0.00			0.09	0.07	0-3
Ulmus	0.00			0.00			0.00			0.00		
	χ^2	df	p	χ^2	df	p	χ^2	df	p	χ^2	df	p
K-W	60.5	6	★★★	111.1	6	★★★	177.9	6	★★★	163.4	6	★★★

Table 6.5. Characteristics of study species; adult tree density (trees per hectare, Chapter 2), total seed mass (mg dry weight per seed, Chapter 3), total seedling mass (mg dry mass per seedling, Chapter 5) and viable seed production (seeds per hectare). Results of Pearson sample correlations, for the association between species characteristics and mean "Persistent", "Germinant" (1996 and 1997) and total seedling density m^{-2} (Table 6.4) are included. Significance levels (p) were ≥0.05 (n.s., not significant) and <0.01 (✶✶).

Taxon		Adult density (trees ha^{-1})	Seed mass (mg dwt)	Seedling mass (mg dwt)	Viable seed production (seeds ha^{-1} $x10^3$)
Acer		69.6	___	44.30	___
Betula		88.6	0.20	0.60	14922.8
Fraxinus		91.6	51.70	25.30	991.9
Ilex		2.2	20.35	12.10	0.6
Sorbus		2.1	3.80	___	0.3
Taxus		3.2	48.20	___	37.4
Ulmus		28.7	9.80	2.90	1.0
"Persistent"	r	0.568	0.658	0.338	-0.142
	df	5	4	3	4
	p	n.s.	n.s.	n.s.	n.s.
"Germinant"96	r	0.608	-0.418	-0.420	0.999
	df	5	4	3	4
	p	n.s.	n.s.	n.s.	✶✶
"Germinant"97	r	0.562	-0.437	-0.492	1.000
	df	5	4	3	4
	p	n.s.	n.s.	n.s.	✶✶
Total	r	0.638	-0.375	-0.427	0.994
	df	5	4	3	4
	p	n.s.	n.s.	n.s.	✶✶

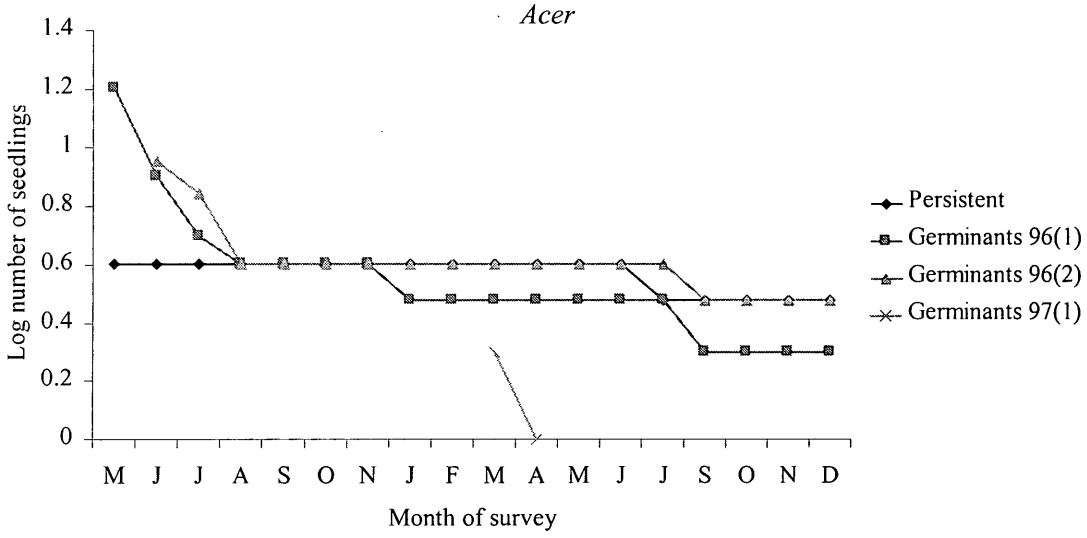
6.3.3 **Patterns of seedling survival**

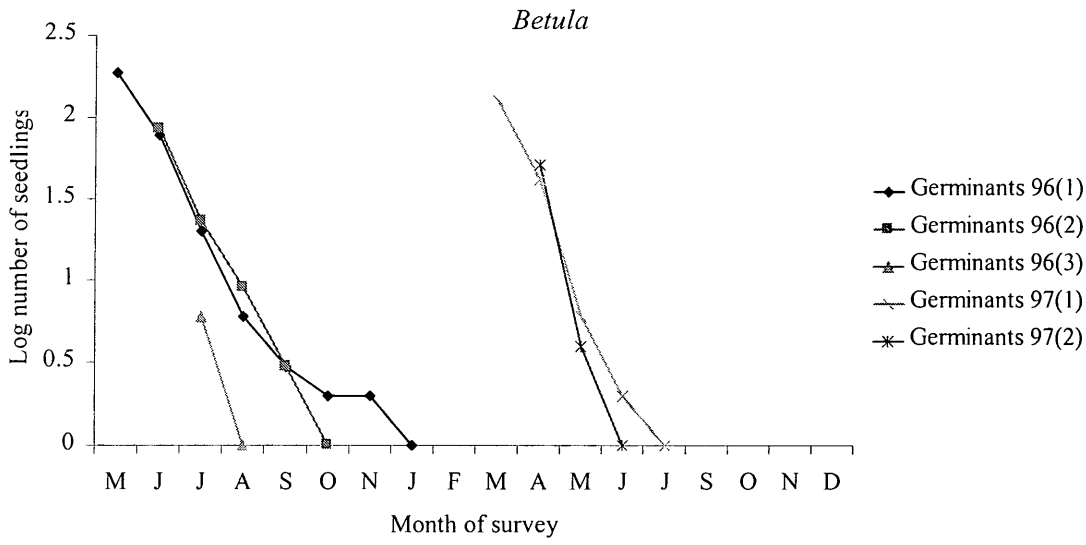
The survivorship of "Germinant" seedlings varied significantly between tree species (Table 6.6). Seedlings of *Betula*, *Ilex*, *Sorbus* and *Taxus* had median survival times of 0 days, since the majority of seedlings did not survive until the survey following their first encounter, and maximum survival times of 195, 97, 37 and 0 days, respectively. None of the seedlings of these taxa germinating in spring and summer 1996 survived beyond November of that year and none of the *Betula* and *Sorbus* seedlings germinating the following spring survived beyond July 1997 (Figure 6.1). The survivorship of *Acer* and *Fraxinus* seedlings was significantly greater, with median survival times of 29 and 101 days, respectively, and maximum survival times exceeding the 576 days of the survey and including a period of over-winter survival.

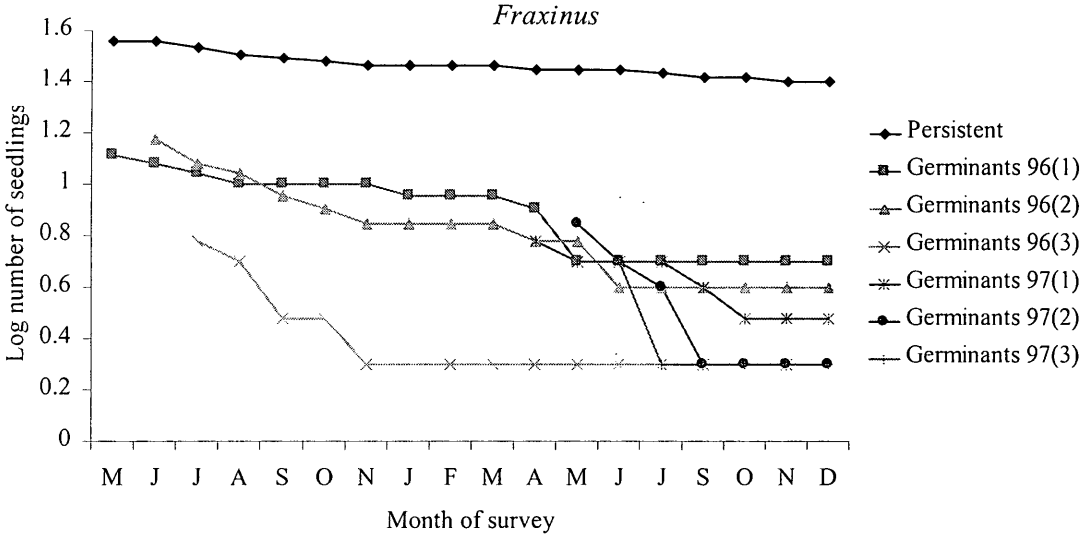
Table 6.6. Results of Kaplan-Meier analysis of seedling survival. Seedlings 'censored' by the analysis were those still surviving at the end of the survey period. Included are standard errors (S.E.), range values and results of Log rank tests for the equality of survival distributions between species (degrees of freedom, df; significance level, *p*).

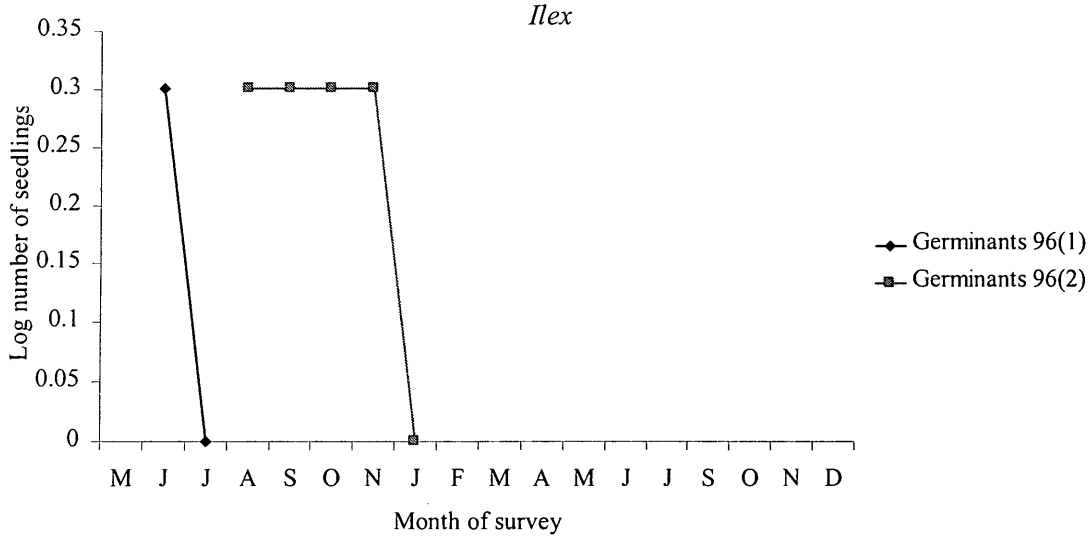
Taxon	Total number of seedlings	Number of seedlings 'censored'	Median survival time (days)	S.E. (days)	Range
Acer	24	3	29	--	0-576+
Betula	448	0	0	--	0-195
Fraxinus	46	12	101	29	0-576+
Ilex	2	0	0	--	0-97
Sorbus	7	0	0	--	0-37
Taxus	3	0	0	--	0
	Log rank test statistic=123.21		df=5	$p<0.001$	

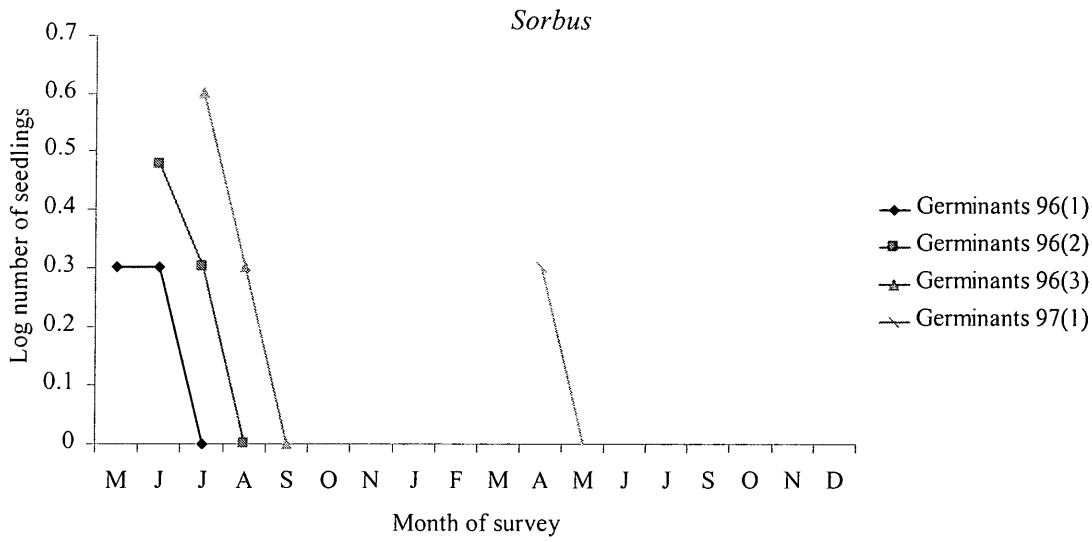
Figure 6.1. The log number of "Persistent" and "Germinant" seedlings of *Acer*, *Betula*, *Fraxinus*, *Ilex*, *Sorbus* and *Taxus*, recorded over the survey period (May, 1996-December, 1997). Individual cohorts of "Germinant" seedlings in 1996 (96(1), 96(2) and 96(3)) and 1997 (97(1), 97(2) and 97(3)) are distinguished.

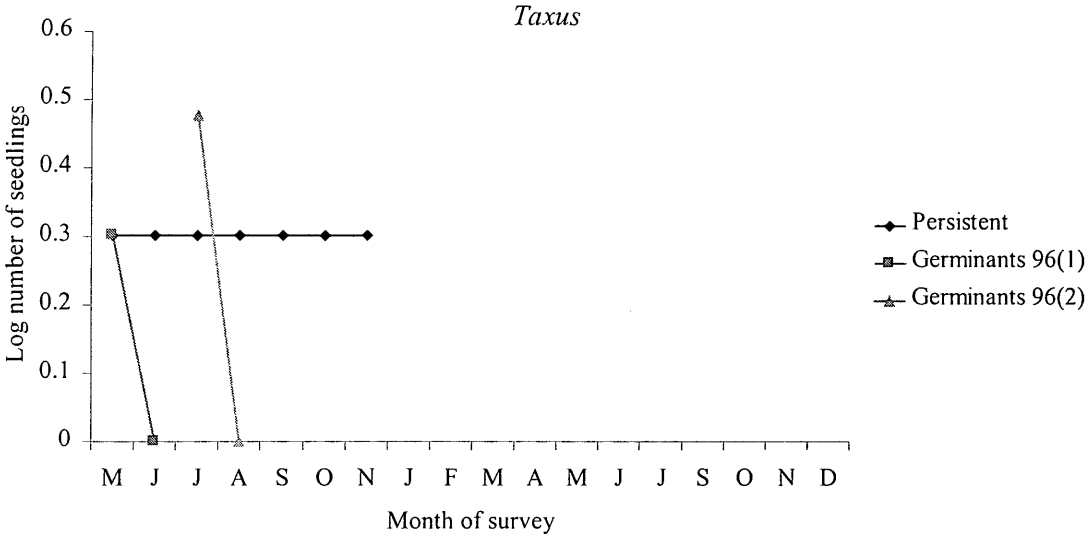



Betula
Log number of seedlings
2.5
2
1.5
1
0.5
0
M J J A S O N J F M A M J J S O N D
Month of survey
Germinants 96(1)
Germinants 96(2)
Germinants 96(3)
Germinants 97(1)
Germinants 97(2)


Fraxinus
Log number of seedlings
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
M J J A S O N J F M A M J J S O N D
Month of survey
Persistent
Germinants 96(1)
Germinants 96(2)
Germinants 96(3)
Germinants 97(1)
Germinants 97(2)
Germinants 97(3)


Ilex
Log number of seedlings
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
M J J A S O N J F M A M J J S O N D
Month of survey
Germinants 96(1)
Germinants 96(2)





Seedlings of *Acer*, *Betula*, *Fraxinus* and *Sorbus* germinated in both years of the survey. Although the density of seedlings (Table 6.4) and the timing of germination (*Acer*, May-June, 1996 and March, 1997; *Betula*, June-July, 1996 and March-April, 1997; *Fraxinus*, May-July, 1996 and April-June, 1997; *Sorbus*, June-July, 1996 and April, 1997; Figure 6.1) varied between 1996 and 1997, the survival distributions of each taxon were not significantly different between years (Table 6.7). Seedlings of all study species germinated in successive cohorts in 1996 (Figure 6.1), although the survival distributions of each species were not significantly different between cohorts (Table 6.8). Similarly, the survival distributions of cohorts of *Fraxinus* seedlings germinating in 1997, were not significantly different. Although the median survival time of *Betula* seedlings was the same between cohorts germinating

in 1997, the survival distributions of cohorts were significantly different. A greater proportion of seedlings of cohort 97(2), than seedlings of cohort 97(1), had survival times of 0 days (94 and 68%, respectively). In addition, survival times of cohort 97(2) seedlings were no greater than 32 days, whereas, seedlings of cohort 97(1) had survival times of up to 101 days. Although seedlings that germinated later generally had shorter survivorship, seedlings of neither cohort survived beyond July of that year. As such, time of germination had no influence on ultimate survivorship patterns.

Table 6.7. Results of Kaplan-Meier analysis of seedling survival and Log rank tests for the equality of survival distributions between years, for each species. Significance levels (p) were ≥0.05 (n.s., not significant).

Taxon	Year	Total number of seedlings	Number of seedlings 'censored'	Median survival time (days)	S.E. (days)
Acer	1996	23	3	29	23
	1997	1	0	0	--
		Log rank test statistic=1.18		df=1	p=n.s.
Betula	1996	273	0	0	--
	1997	175	0	0	--
		Log rank test statistic=0.36		df=1	p=n.s.
Fraxinus	1996	31	8	195	116
	1997	15	4	69	44
		Log rank test statistic=2.48		df=1	p=n.s.
Sorbus	1996	6	0	0	--
	1997	1	0	0	--
		Log rank test statistic=0.75		df=1	p=n.s.

Table 6.8. Results of Kaplan-Meier analysis of seedling survival and Log rank tests for the equality of survival distributions between cohorts of each species (96(1), Cohort 1, 1996; 96(2), Cohort 2, 1996; 96(3), Cohort 3, 1996; 97(1), Cohort 1, 1997; 97(2), Cohort 2, 1997; 97(3), Cohort 3, 1997). Significance levels (p) include ≥0.05 (n.s., not significant).

Taxon	Cohort	Total number of seedlings	Number of seedlings 'censored'	Median survival time (days)	S.E. (days)
Acer	96(1)	15	1	0	--
	96(2)	8	2	32	15
		Log rank test statistic=2.07		df=1	p=n.s.
Betula	96(1)	185	0	0	--
	96(2)	83	0	0	--
	96(3)	5	0	0	--
		Log rank test statistic=2.85		df=2	p=n.s.
	97(1)	125	0	0	--
	97(2)	50	0	0	--
		Log rank test statistic=21.31		df=1	p<0.001
Fraxinus	96(1)	12	4	343	19
	96(2)	14	3	102	60
	96(3)	5	1	37	20
		Log rank test statistic=1.63		df=2	p=n.s.
	97(1)	5	2	137	39
	97(2)	6	1	35	28
	97(3)	4	1	0	--
		Log rank test statistic=1.47		df=2	p=n.s.
Ilex	96(1)	1	0	0	--
	96(2)	1	0	97	--
		Log rank test statistic=1.00		df=1	p=n.s.
Sorbus	96(1)	1	0	29	--
	96(2)	2	0	0	--
	96(3)	3	0	0	--
		Log rank test statistic=0.13		df=2	p=n.s.
Taxus	96(1)	1	0	0	--
	96(2)	2	0	0	--
		Log rank test statistic= --		df=2	p=n.s.

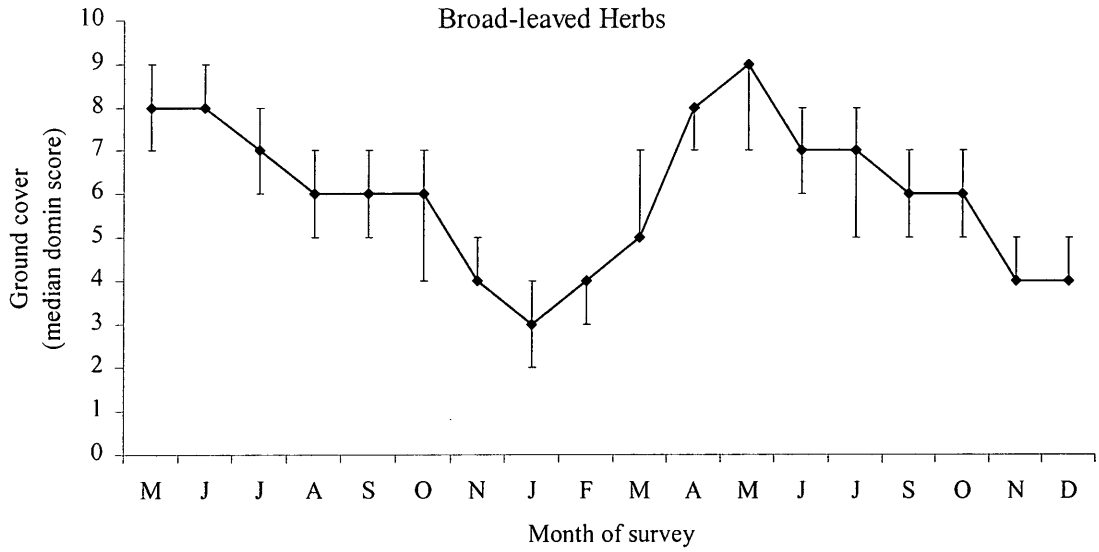
6.3.4 **Dynamics of principal field layer components**

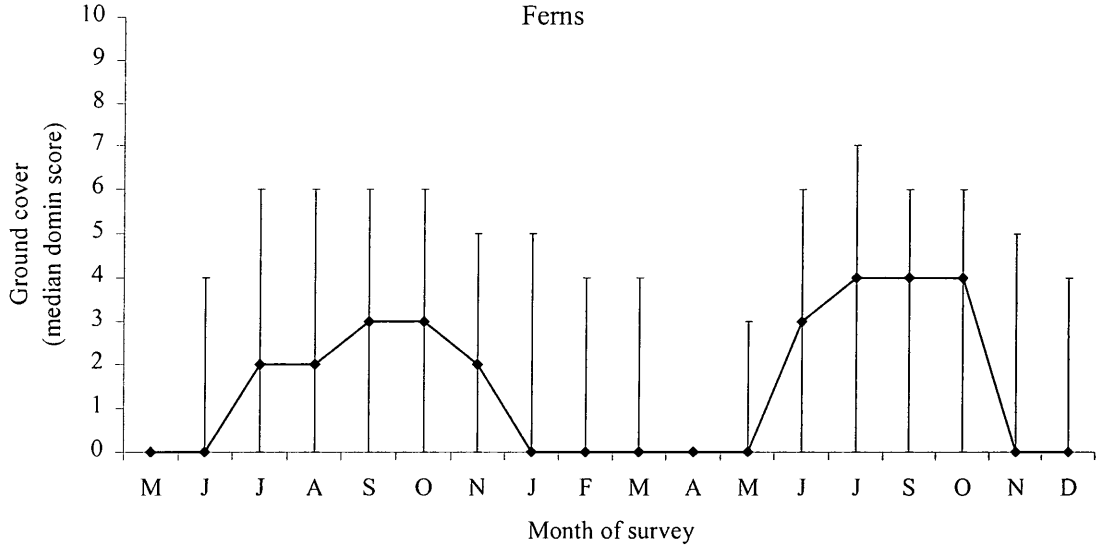
Although the cover and composition of the field layer was extremely dynamic over the survey period (Figure 6.2), there were seasonal patterns that were broadly similar between years. Between April and June, the cover of broad-leaved herbs was at its greatest, while the cover of fern, shrub and leaf litter was low. Between July and

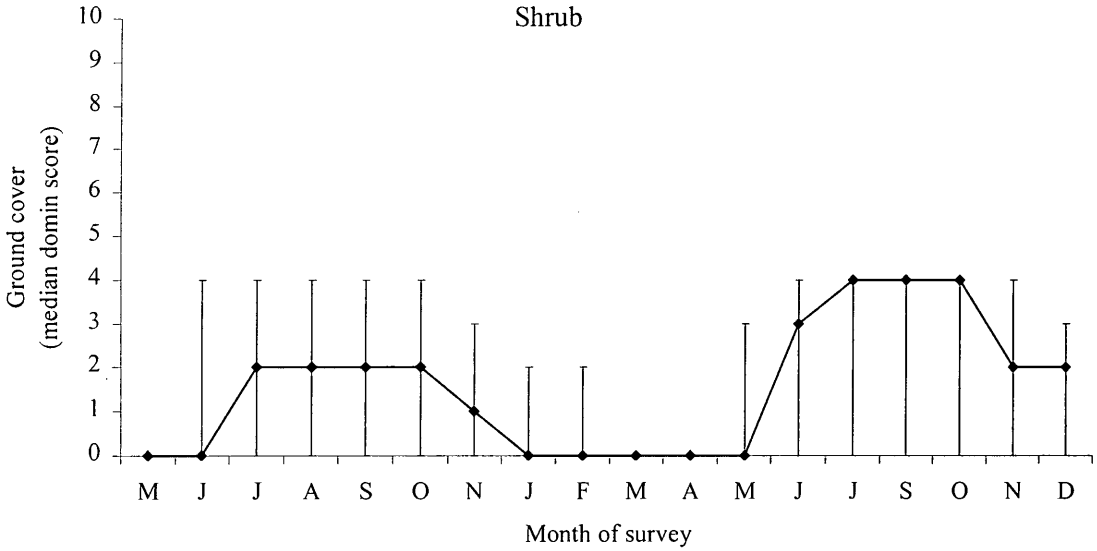
October, the cover of broad-leaved herbs declined, the cover of leaf litter increased and the cover of fern and shrub reached its maximum. Between November and March, the cover of leaf litter was at its greatest, while the cover of broad-leaved herbs, fern and shrub was low. The median cover of graminoids was stable throughout the survey period. The cover of mosses was also relatively stable, although was at its lowest when the cover of broad-leaved herbs was at its highest. Throughout the survey, bare ground was a minor component of the field layer, having a median domin cover score of zero. Overall, the field layer could be described as broad-leaved herb dominated in the spring, leaf litter dominated in the winter and of mixed composition in the summer and autumn.

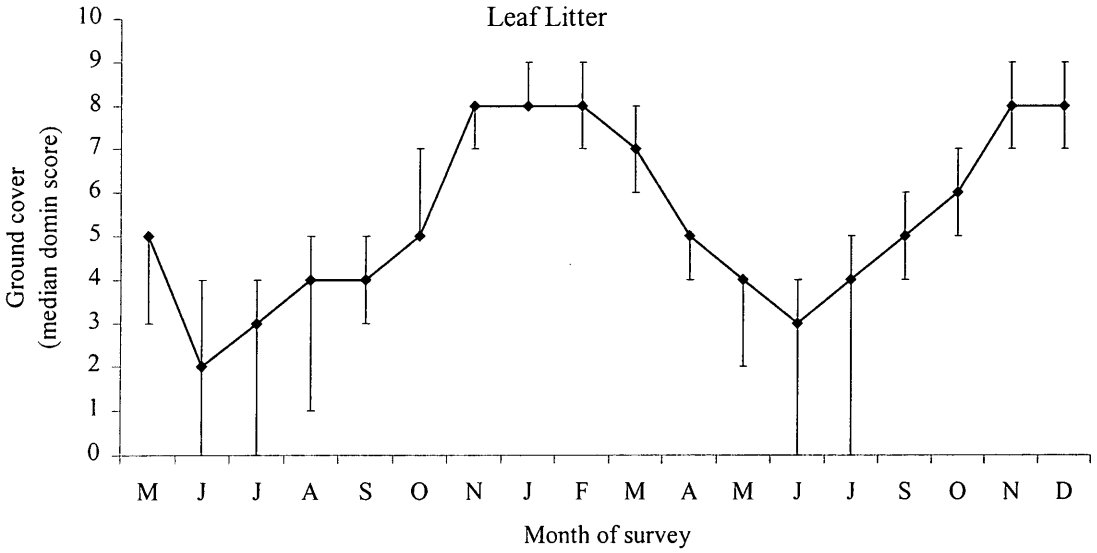
The cover of broad-leaved herbs, leaf litter and moss was more evenly distributed across the site than the cover of ferns, shrub, graminoids and bare ground, as reflected by interquartile ranges. Differences between quadrats also varied seasonally for leaf litter, which was more evenly distributed in winter at peak cover, and graminoids, which were more evenly distributed in spring/summer, even though median cover was stable throughout the year.

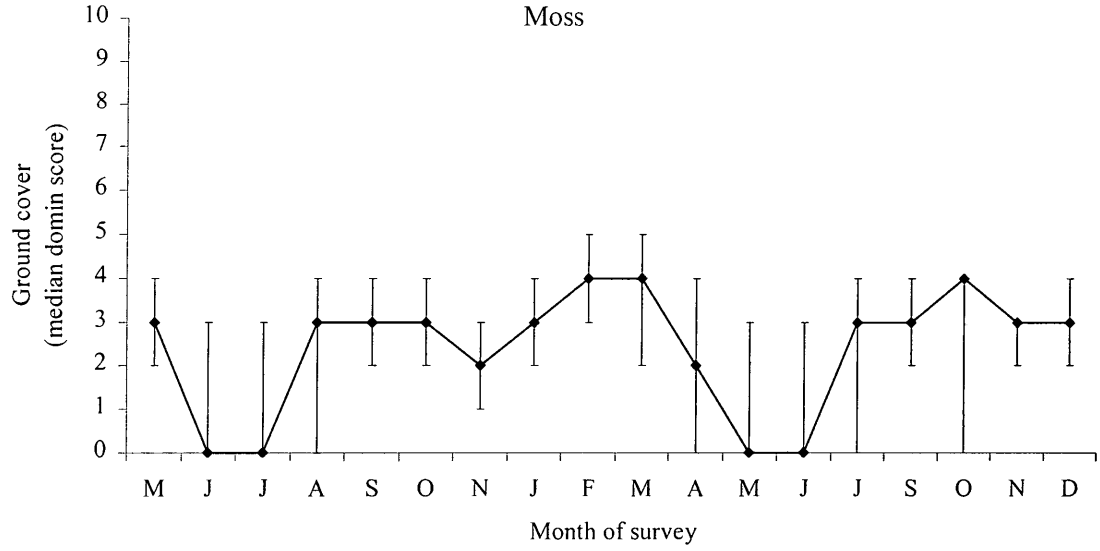
Figure 6.2. The ground cover (median domin score ± interquartile range) of broad-leaved herbs, ferns, shrub, leaf litter, moss, graminoids and bare ground, recorded over the study period (May, 1996-December, 1997).

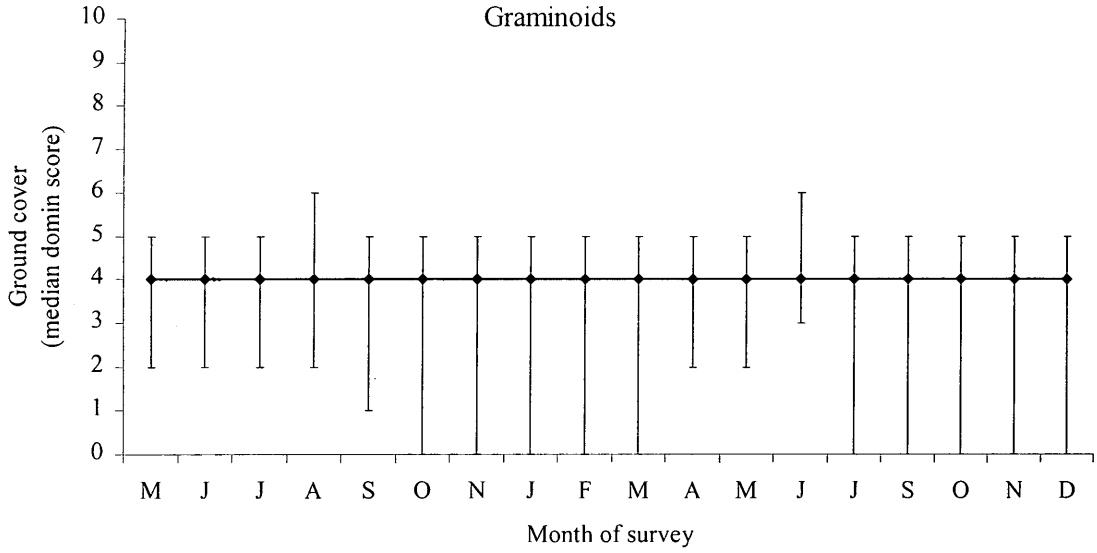


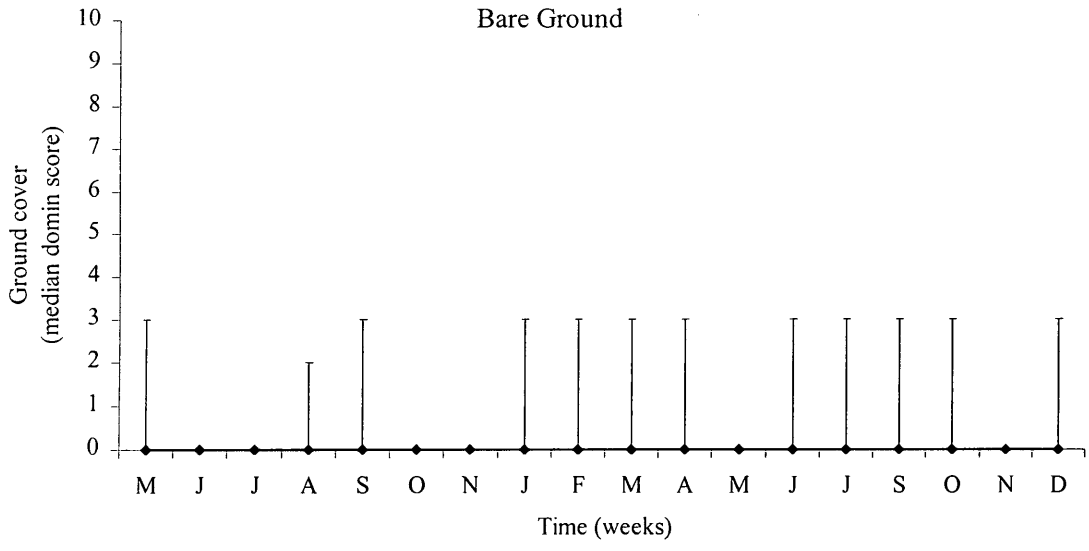

Ferns
Ground cover
(median domin score)
10
9
8
7
6
5
4
3
2
1
0
M J J A S O N J F M A M J J S O N D
Month of survey


Shrub
Ground cover
(median domin score)
10
9
8
7
6
5
4
3
2
1
0
M J J A S O N J F M A M J J S O N D
Month of survey


Leaf Litter
Ground cover
(median domin score)
10
9
8
7
6
5
4
3
2
1
0
M J J A S O N J F M A M J J S O N D
Month of survey


Moss
Ground cover
(median domin score)
10
9
8
7
6
5
4
3
2
1
0
M J J A S O N J F M A M J J S O N D
Month of survey


Graminoids
Ground cover
(median domin score)
10
9
8
7
6
5
4
3
2
1
0
M J J A S O N J F M A M J J S O N D
Month of survey


Bare Ground
Ground cover
(median domin score)
10
9
8
7
6
5
4
3
2
1
0
M J J A S O N J F M A M J J S O N D
Time (weeks)

6.3.5 **Environmental correlates of seedling distribution**

As a result of sample size constraints, meaningful analysis of seedling distribution was limited to *Acer*, *Betula* and *Fraxinus*. Canonical Correspondence Analysis (CCA) resulted in the maximum dispersion of seedling data along axes representing linear combinations of the environmental variables. The first, second, third and fourth canonical axes generated eigen values of 0.481, 0.299, 0.223 and 0.192, respectively, accounting for 30.0, 18.7, 14.0 and 11.9 per cent of the variance in seedling data, respectively. A Monte Carlo permutation test confirmed the statistical significance of the first canonical axis ($p \leq 0.001$) and the overall species-environment association ($p \leq 0.001$). Since the first and second axes accounted for nearly fifty per cent of the variance in species data, and the third and fourth axes only contributed a further twenty-six per cent of variance, subsequent analysis will principally consider the first two axes.

The dispersion of seedling scores, environmental variable scores and state variable scores were examined by graphical ordination with respect to the primary and secondary canonical axes. The dispersion of scores representing the number of seedlings per quadrat was broadly similar to the dispersion of scores representing the proportion of the original cohort surviving (Figure 6.3).

CCA distinguished cohorts of tree seedlings on the first axis (Figure 6.3). 'Young' seedlings (New germinants and Last survey seedlings) had positive scores on axis 1, whereas 'Old' seedlings (This season and Previous season+ seedlings) had negative scores. The second canonical axis distinguished species of tree seedling. *Acer* seedlings had high positive scores on axis 2, *Fraxinus* seedlings had negative scores and *Betula* seedlings had intermediate positive scores.

Biplot scores of environmental variables were represented by vectors in the direction of maximum change of each variable (Figure 6.4). Vector length reflected the rate of change of each environmental variable in that direction, and the strength of correlation with the ordination axes and patterns of seedling data. CCA distinguished groups of state variables on both primary and secondary canonical axes (Figure 6.5). State variables S2, S3, S11 and S12 had high positive scores on axis 1, whereas S1, S4-S9, S10 and S13-17 had negative scores. State variables S1-S9 had positive scores on axis 2, whereas S10-S17 had negative scores.

Figure 6.3. CCA ordination of seedling scores
(Value labels on page 137, Table 6.1).

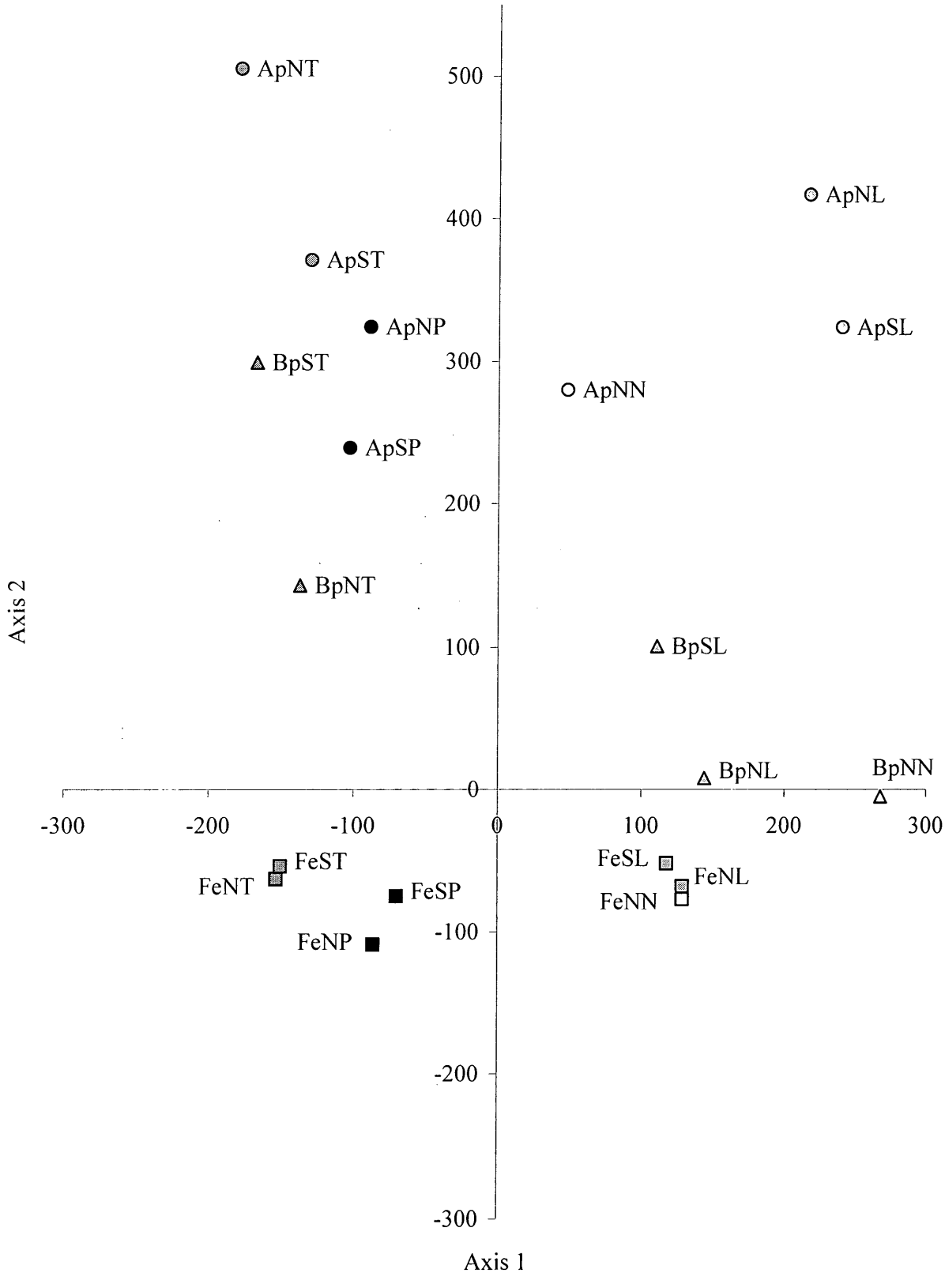
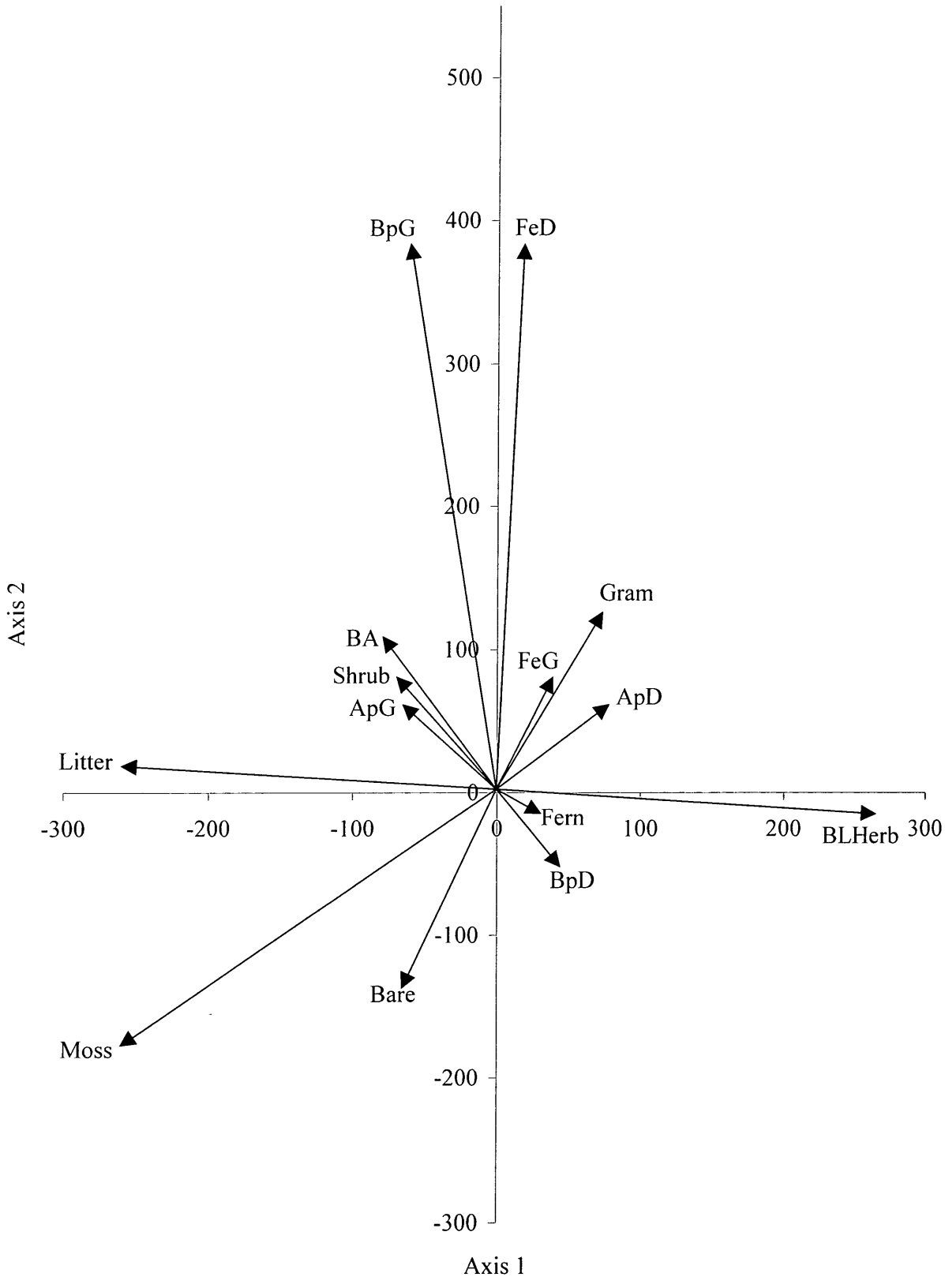


Figure 6.4. CCA ordination of environmental variable scores
(Value labels on page 138, Table 6.2).



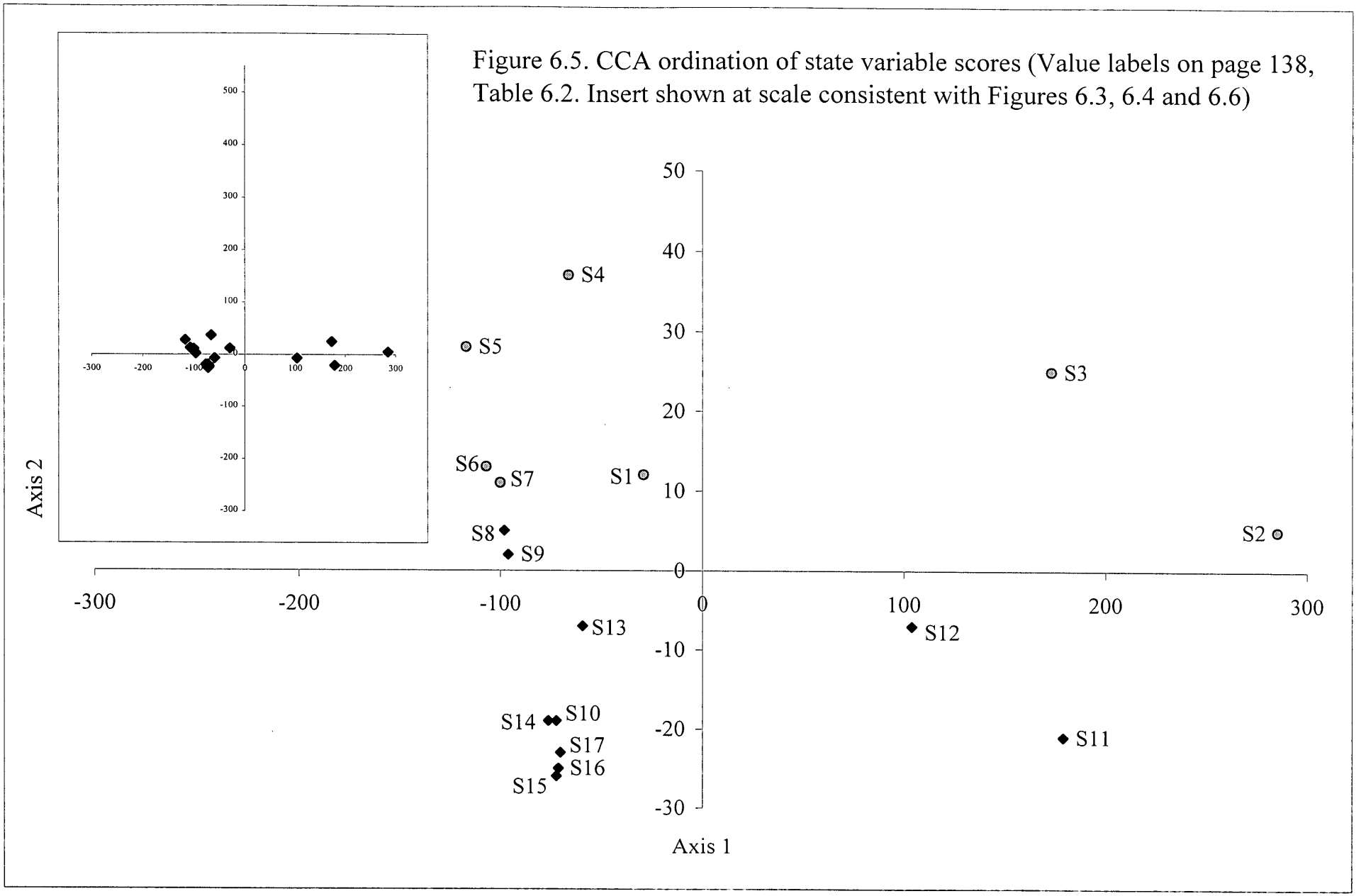


Figure 6.5. CCA ordination of state variable scores (Value labels on page 138, Table 6.2. Insert shown at scale consistent with Figures 6.3, 6.4 and 6.6)

The contribution of each environmental and state variable was determined by regression with each canonical axis (Table 6.9). Of the available variables, FeG was correlated with axis 1 only, S4, S5, S6, S13, S14, BA, FeD, Fern and Gram with axis 2 only and S1, S2, S3, S11, S12, BpD, BpG, BLHerb and Moss with both axes. Figure 6.6 shows the combined ordination of statistically significant environmental and state variables, and seedling scores for cohorts of each species. BpG, FeD, BLHerb, Moss, bA and Gram were the principal environmental variables correlated with patterns of seedling data.

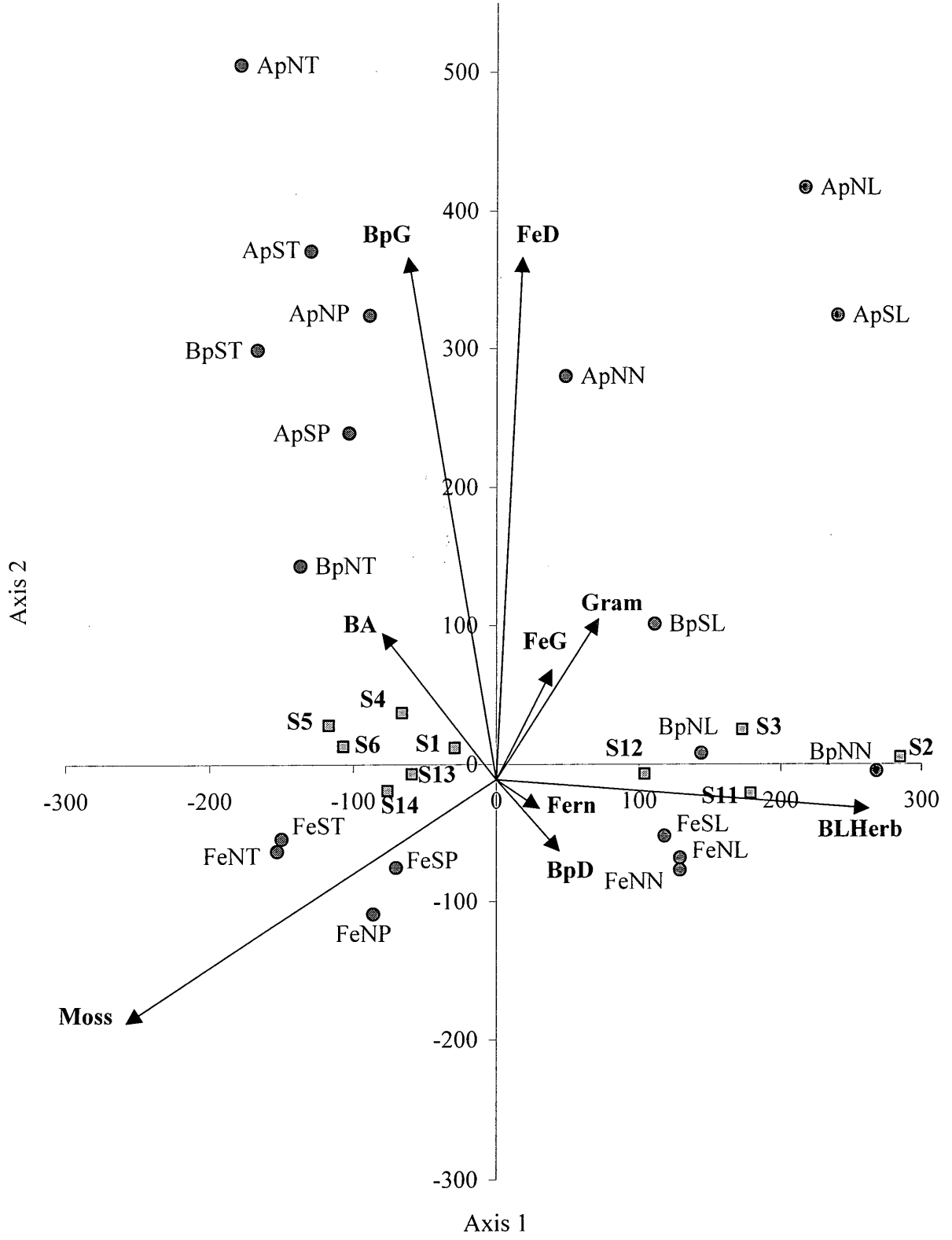
Young seedlings of all species were principally associated with high broad-leaved herb cover and low moss cover in June (S2) and July (S3), 1996, and April (S11) and May (S12), 1997 (Figures 6.2 and 6.6). In contrast, Old seedlings were principally associated with low broad-leaved herb cover and high moss cover in May (S1), August (S4), September (S5) and October (S6), 1996, and June (S13) and July (S14), 1997. The negative association between broad-leaved herb and moss cover, was confirmed by statistical correlation (r= -0.343, df=808, $p<0.01$). The cover of graminoids also influenced patterns of seedling data (Figure 6.6). Seedlings of *Acer* were most associated with high graminoid cover, whereas, Old seedlings of *Fraxinus* were most associated with low graminoid cover. *Betula* seedlings and Young seedlings of *Fraxinus* were either less influenced by graminoids, or were associated with intermediate cover. Such associations were most likely spatial, rather than temporal, since the cover of graminoids was similar throughout the survey period (Figure 6.2).

Distance to the nearest adult of *Fraxinus* was negatively correlated with distance to the nearest adult of *Betula* (r= -0.143, df=808, $p<0.01$) and positively correlated with the girth of the nearest adult of *Betula* (r=0.609, df=808, $p<0.01$) (Figure 6.6). Seedlings of *Acer* were associated with large adults of *Betula* (high BpG) and distant adults of *Fraxinus* (high FeD). In contrast, seedlings of *Fraxinus* were associated with small adults of *Betula* (low BpG) and proximate adults of *Fraxinus* (low FeD). *Betula* seedlings were either unaffected by conspecific girth and distance to *Fraxinus,* or were associated with intermediate measures.

Table 6.9. Regression/canonical coefficients (C) for the association between independent variables and the first two canonical axes. T-values (T) and significance levels (p) are included; $p \geq 0.05$ (n.s., not significant), $p<0.05$ (✶). All values are absolute, having taken account of CCA multipliers.

	Axis 1			Axis 2		
Variable	C	T	p	C	T	p
S1	1.05	3.2	✶	0.91	2.9	✶
S2	6.79	13.7	✶	1.55	3.3	✶
S3	4.73	10.2	✶	1.51	3.5	✶
S4	0.58	1.5	n.s.	1.21	3.4	✶
S5	-0.37	-1.1	n.s.	1.03	3.2	✶
S6	-0.41	-1.3	n.s.	0.67	2.3	✶
S7	-0.6	-2	n.s.	0.14	0.5	n.s.
S8	-0.47	-1.6	n.s.	0.02	0.1	n.s.
S9	-0.18	-0.6	n.s.	0.09	0.3	n.s.
S10	0.27	0.9	n.s.	0.23	0.8	n.s.
S11	5.01	12.3	✶	0.96	2.5	✶
S12	3.45	8.4	✶	1.15	3	✶
S13	0.38	1.1	n.s.	0.9	2.7	✶
S14	0.12	0.4	n.s.	0.69	2.3	✶
S15	0.15	0.5	n.s.	0.59	2	n.s.
S16	0.06	0.2	n.s.	0.4	1.5	n.s.
S17	-0.16	-0.6	n.s.	0	0	n.s.
BA	-0.08	-0.3	n.s.	0.94	3.8	✶
Ap D	0.23	0.8	n.s.	-0.01	0	n.s.
Bp D	-0.8	-2.8	✶	0.68	2.6	✶
Fe D	0.36	1.1	n.s.	3.63	11.5	✶
Ap G	-0.31	-1.2	n.s.	-0.29	-1.2	n.s.
Bp G	-1.79	-5	✶	2.74	8.1	✶
Fe G	0.85	3.6	✶	0.31	1.4	n.s.
BL Herb	-0.85	-2.3	✶	-2.39	-6.9	✶
Shrub	-0.48	-1.5	n.s.	-0.15	-0.5	n.s.
Fern	0.2	0.7	n.s.	-1.46	-5.2	✶
Gram	-0.31	-1	n.s.	0.67	2.4	✶
Moss	-2.95	-8.1	✶	-0.97	-2.8	✶
Litter	-0.08	-0.2	n.s.	0.12	0.3	n.s.
Bare	0.21	0.7	n.s.	-0.53	-1.9	n.s.

Figure 6.6. Combined CCA ordination of seedling scores and statistically significant environmental and state variables (Value labels on page 137, Table 6.1 and page 138, Table 6.2).



The local density of adult trees, taken as basal area (BA), also influenced patterns of seedling data. Young seedlings of *Betula* and *Fraxinus* were most associated with low basal area, whereas, *Acer* seedlings and Old *Betula* seedlings were most associated with high basal area. Old *Fraxinus* seedlings were either unaffected by local tree density, or were associated with intermediate basal area. Basal area was negatively correlated with Fern cover ($r = -0.318$, $df = 808$, $p < 0.01$) and positively correlated with the cover of graminoids ($r = 0.098$, $df = 808$, $p < 0.01$) and moss ($r = 0.347$, $df = 808$, $p < 0.01$). Broad-leaved herb cover was not significantly associated with canopy basal area ($r = -0.058$, $df = 808$, $p =$ n.s.).

Variation between years in seasonal patterns of field layer cover (Figure 6.2) and the frequency and timing of seedling germination (Table 6.4, Figure 6.1), were reflected in the dispersion of state variables on the second canonical axis (Figure 6.6). May to October 1996 (S1-S6) had positive scores on axis 2, whereas, April to July, 1997 (S11-S14) had negative scores.

6.4 DISCUSSION

6.4.1 **Patterns of seedling regeneration**

Seedling regeneration involves a continuous multi-step sequence of events, including seed production, dispersal, survival and germination, and seedling emergence, growth, survival and establishment. In the present study, variation between tree species in natural seedling density represented differences in one or more aspects of this sequence.

Variation between species in the density of "Germinant" seedlings, which made up the vast proportion of the total per quadrat, was correlated with the abundance of viable seed produced in 1997 (Table 6.5). Differences in seed dispersal, seed survival and seedling germination were not sufficient to influence the association between viable seed output and seedling emergence. Since the density of "Persistent" seedlings, of at least one year old, was not correlated with viable seed production, seedling density subsequent to emergence was most likely determined by alternative factors.

The survivorship of "Germinant" seedlings varied significantly between taxa, although it was similar between cohorts of each taxon and between years for *Acer*, *Betula*, *Fraxinus* and *Sorbus* (Table 6.6), reflecting the consistency of survival characteristics of each taxon.

The regeneration characteristics of each tree species, as summarised in Table 6.10, can be distinguished in terms of viable seed output, seedling survivorship and the abundance of "Germinant" and "Persistent" seedlings. *Betula* produced vast numbers of viable seeds and "Germinant" seedlings, although seedling survivorship was low and no "Persistent" seedlings were encountered. *Acer* and *Fraxinus* produced fewer viable seeds and "Germinant" seedlings, although seedling survivorship and the abundance of "Persistent" seedlings were much greater. Nakashizuka *et al.* (1995) also recorded a negative association between seedling survival and the abundance of seeds produced, reflecting a strong negative correlation between seed crop size and seed size, and a positive correlation between seed size and seedling survival. Melzack & Watts (1982) found that seed size was positively associated with germination rates and seedling size. *Ilex*, *Sorbus*, *Taxus* and *Ulmus*, however, produced few viable seeds and "Germinant" seedlings, which were of low survivorship, and few "Persistent" seedlings.

Table 6.10. Summary of the regeneration characteristics of each study species recorded in the present study.

Taxon	Viable seed production	"Germinant" seedlings 1996	1997	Seedling survivorship	"Persistent" seedlings
Acer	-----	Occasional	Rare	High	Rare
Betula	Very high	Numerous	Numerous	Low	Absent
Fraxinus	High	Occasional	Rare	Very high	Occasional
Ilex	Low	Rare	Absent	Low	Absent
Sorbus	Low	Rare	Rare	Low	Absent
Taxus	Low	Rare	Absent	Low	Rare
Ulmus	Low	Absent	Absent	-----	Absent

Consistent with variation between tree species, differences between years in the density of "Germinant" seedlings was most likely associated with variation in viable seed output. Mast seeding is common amongst temperate tree species (Sharp & Sprague, 1967; Gardner, 1977; Harper, 1977; Jensen, 1982) and involves intermittent years of high, synchronous seed production within a population, separated by long periods when few seeds, if any, are set. Punctuated seedling recruitment typically follows masting behaviour (Evans, 1988). Unfortunately, estimates of seed crops from which "Germinant" seedlings emerged in 1996 and 1997, were not available for comparison.

Annual variation in the density of "Germinant" seedlings may have also resulted from differences in seed dispersal, seed survival or seedling germination between viable seed production and seedling emergence. For example, Tapper (1992) found that an unusually cold winter followed by late snow melt and a cold and wet spring, was sufficient to reduce the germination of *Fraxinus excelsior* to six per cent of that expected.

Viable seed output in 1997 was correlated with the density of "Germinant" seedlings, which germinated from seeds produced at least one year prior to their emergence in 1996 and 1997. Relative differences between species in viable seed output and seedling emergence were, therefore, broadly similar between years. The production of viable seeds and emergence of seedlings of *Betula* would have been consistently greater than that of *Acer* and *Fraxinus*. Viable seeds and emergent seedlings of *Ilex*, *Sorbus*, *Taxus* and *Ulmus* would have been consistently sparse. Although not formally quantified, observations made during the study period would support such patterns. Tapper (1992) found that the absolute density of *Fraxinus*

seedlings emerging was positively correlated with total seed production two years previously.

6.4.2 **Environmental correlates of seedling distribution**

Although viable seed output determined overall rates of seed germination and seedling emergence, alternative factors influenced the subsequent survival and establishment of seedlings. Spatial associations between seedling recruitment and a number of habitat characteristics were identified following the analysis of seedling distribution using CCA, as summarised in Table 6.11. The dispersion of scores representing the number of seedlings per quadrat was broadly similar to the dispersion of scores representing the relative survival of seedlings (Figure 6.3). The spatial distribution of seedling density was, therefore, associated with the spatial distribution of seedling survival.

Table 6.11. Summary of associations between seedling recruitment and habitat characteristics, including girth of nearest adult neighbour of Betula (BpG), distance to nearest adult neighbour of Fraxinus (FeD), total basal area of adult trees in vicinity of quadrat (BA) and the cover of graminoids (Gram), Moss and broad-leaved herbs (BLHerbs).

Taxon	Seedling age	BpG	FeD	BA	Gram	BLHerb	Moss
Acer	Young	High	High	High	High	High	Low
	Old	High	High	High	High	Low	High
Betula	Young	Medium	Medium	Low	Medium	High	Low
	Old	Medium	Medium	High	Medium	Low	High
Fraxinus	Young	Low	Low	Low	Medium	High	Low
	Old	Low	Low	Medium	Low	Low	High

Patterns of seedling recruitment recorded in the present study were generally consistent with the regeneration characteristics of each species in temperate deciduous woodland (Table 2.1). High rates of mortality followed seed germination and seedling emergence in the spring, when shallow rooted seedlings were particularly susceptible to mortality factors during active growth (Peterken, 1966). Seedlings surviving until winter, when mortality rates were reduced, had a greater expectancy of life (Tapper, 1992).

Rather than occurring randomly, seedling regeneration was associated with specific habitat characteristics. The distribution of Young seedlings was distinct from

that of Old seedlings, indicating that seed germination, seedling emergence and early seedling survival occurred in habitats that were unsuitable for subsequent establishment and survival.

Young seedlings of *Acer*, *Betula* and *Fraxinus* were associated with high broad-leaved herb cover and low moss cover. Since tree seeds are particularly vulnerable to desiccation, the cover provided by broad-leaved herbs may have increased rates of seed germination by depressing critical water loss (Watt, 1919, 1923; Wood, 1938; Shaw, 1968b; Pigott, 1983). Broad-leaved herb cover was not sufficiently dense to limit the germination of light-demanding taxa, including *Betula* (Watt, 1919; Pigott, 1983; Goldberg, 1985), or prevent seeds from reaching the soil (Watt, 1919). Greater stability of soil surface temperature may also account for higher rates of seed germination, seedling emergence and early seedling survival beneath broad-leaved herb cover (Wood, 1938).

Old seedlings of *Acer*, *Betula* and *Fraxinus* were associated with low broad-leaved herb cover and high moss cover. The shading effect of the herb layer may have directly inhibited seedling development, establishment and survival (Tapper, 1992). *Betula* is a shade intolerant pioneer tree which regenerates most profusely on open mineral soil of moderate phosphate status (Evans, 1988), often with continuous moss cover or a thin layer of tree litter (Grime *et al.*, 1988). *Fraxinus* seedlings are also intolerant of dense field layer shade (Wardle, 1961), establishing most typically on relatively open, moist, well drained, base-rich sites with thin litter layers (Grime *et al.*, 1988; Peltier *et al.*, 1997). Broad-leaved herbs may also limit recruitment by the interception of precipitation (Linhart & Whelan, 1980), the removal of moisture and nutrients from the soil (Evans, 1988), the smothering and toxic action of decaying plant material overlying seedlings (Watt, 1919) and the harbouring of seed and seedling predators (Chapters 3 & 5). Field layer shade may also suppress the growth and development of *Fraxinus* seedlings and increase susceptibility to inter-seedling competition (Tapper, 1992). *Fraxinus* often regenerates where soil instability, soil dryness, canopy cover or excessive wetness restrict the herb layer and allow seedlings to become established (Wardle, 1959, 1961).

Seedlings of *Acer* are widely distributed on bare or lightly shaded, basic, low disturbance soils of adequate phosphate, moisture and depth (Evans, 1988; Grime *et al.*, 1988). Although *Acer* regenerates profusely beneath moderately deep shade in association with shade herb species, seedlings are intolerant of competition and may

be readily suppressed by field layer vegetation (Jones, 1945). *Acer* seedlings typically establish beneath a thin and discontinuous layer of herbaceous species and litter, often accompanied by mosses and seedlings of *Sambucus nigra*, suggesting that *Acer* is nitrophilous (Jones, 1945; Grime *et al.*, 1988). Seasonal regeneration of *Acer*, *Betula,* and *Fraxinus* most likely benefits from early germination in vegetation gaps, preceding the maximum cover of broad-leaved herbs.

Seedling distribution also varied between tree species, reflecting contrasting associations between seedling recruitment and habitat characteristics. Canopy cover, or a correlated factor, strongly influenced patterns of seed germination and seedling emergence, establishment and survival. The girth of adult *Betula*, distance to adult *Fraxinus* and total basal area were significant attributes of canopy cover and associations between seedling recruitment and canopy cover differed according to seedling age and species.

Although seedlings of *Acer* have been found to germinate profusely beneath dense canopy shade, prolonged growth and survival is improved in thin irregular stands of moderate shade (Jones, 1945). *Acer* is more shade tolerant than *Fraxinus* and often appears as advance regeneration beneath light crowned taxa, including *Fraxinus* (Evans, 1988). In the present study, Young and Old seedlings of *Acer* were associated with high graminoid cover and closed tree canopies containing large adults of *Betula* and distant adults of *Fraxinus*. Such canopies most likely generated moderate to deep shade that was suitable for the germination, establishment and survival of shade tolerant *Acer*, while sufficient to limit herb competition and exclude seedlings of *Betula* and *Fraxinus*. Jones (1945) found that proximity to the seed source was essential to the profuse regeneration of *Acer*, often recording circles of recruitment around fruiting adults. In the present study, the abundance and survival of *Acer* seedlings was not associated with either the girth or distance of conspecific adults, although patterns of fruit production and dispersal were not recorded.

Although banks of *Fraxinus* seedlings are often released by canopy gap formation (Wardle, 1959, 1961; Emborg, 1998), recruitment is most prolific under semi-shade conditions (Peltier *et al.*, 1997). Seedlings of *Fraxinus* may establish beneath considerable canopy cover, despite an intolerance of field layer cover (Tapper, 1992). *Fraxinus* typically regenerates where canopy shade is sufficient to restrict dense layers of herbaceous vegetation that would otherwise exclude *Fraxinus*

seedlings (Wardle, 1959, 1961). Harmer *et al.* (1997) also found that the abundance and vigour of herb growth was inversely related to the extent of the canopy.

In the present study, broad-leaved herb cover was not significantly associated with canopy basal area. However, grass and moss cover were positively associated with basal area and fern cover was negatively associated with basal area. Seedlings of *Fraxinus* were associated with tree canopies containing small adults of *Betula* and proximate adults of *Fraxinus*, reflecting a direct association between seedling density and proximity to the seed source. Such canopies were unlikely to represent pure stands of *Fraxinus*, the cover of which would have been sufficiently thin to favour a dense field layer and the elimination of *Fraxinus* seedlings (Wardle, 1959).

Young seedlings of *Fraxinus* were associated with open canopies, whereas the distribution of Old seedlings was either independent of canopy cover or was associated with intermediate cover. Such patterns reflected the direct and indirect influence of canopy shade on tree seedlings and field layer vegetation (Wardle, 1959, 1961; Harmer *et al.*, 1997). Seed germination, seedling emergence and early seedling survival were associated with open canopies, low grass and moss cover, and high overlying fern cover, providing conditions of greater moisture and stability of soil surface temperature. Subsequent seedling establishment and survival were either independent of canopy cover, and most likely determined by field layer cover, or were associated with intermediate canopy cover. Wardle (1959, 1961) supports the profuse regeneration of *Fraxinus* under semi-shade conditions which favour *Fraxinus* seedlings over the field layer. Sites which favoured the regeneration of *Fraxinus* were unsuitable for the regeneration of *Acer* and *Betula*, most likely resulting from intolerance of herb competition (Jones, 1945) and shade (Pigott, 1983), respectively, beneath intermediate canopy and field layer cover. Although *Fraxinus* seedlings are moderately shade tolerant during early survival, within three or four years seedlings become increasingly dependent on full overhead light for subsequent growth and development (Evans, 1988).

Although the distributions of *Acer* and *Fraxinus* are often closely associated, *Acer* has greater vigour and persistence in the shade (Jones, 1945; Evans, 1988). Consequently, relative light intensity determines which species eventually dominates. Linhart & Whelan (1980) recorded a profusion of *Rubus fruticosus* following protection from browsing pressure. *Acer* regeneration subsequently replaced *Fraxinus*

regeneration as a result increased field layer cover. In the present study, there was no association between seedling distribution and the cover of *Rubus fruticosus*, the principal component of Shrub vegetation.

Light demanding seedlings of *Betula* typically establish beneath openings in both main and understorey canopies (Morgan, 1991), showing a marked dissociation from ungrazed field layers and heavily shaded sites, including canopies of *Acer* (Pigott, 1983). In the present study, the distribution of *Betula* seedlings was either independent of the girth of adult *Betula* and the proximity of adult *Fraxinus*, or was associated with intermediate measures. Specific canopy characteristics may have been less significant to the regeneration of *Betula* than the indirect influence of canopy shade on field layer cover, to which seedlings were particularly sensitive. In addition, any spatial association between seedlings and the seed source may have been obscured by the long distance dispersal of vast quantities of seed.

Young seedlings were associated with low canopy basal area, whereas Old seedlings were associated with high canopy basal area. As with the regeneration of *Fraxinus*, seed germination, seedling emergence and early seedling survival were associated with open canopies, low grass and moss cover, and high overlying fern cover, providing conditions of greater moisture and stability of soil surface temperature. Evans (1988) also reported the emergence of *Betula* seedlings amongst ferns. Subsequent seedling establishment and survival were associated with closed canopies, which favoured light-demanding *Betula* seedlings over the field layer. Cold stress may have been sufficient to exclude seedlings of *Acer* and *Fraxinus* from open sites that were suitable for the recruitment of cold-tolerant *Betula* seedlings (Table 2.1), assuming the abundance and vigour of field layer growth was inversely related to the extent of the canopy (Harmer *et al*, 1997). Greater tolerance of herb competition may have also accounted for the survival of *Betula* seedlings in sites that were unsuitable for the regeneration of *Acer* and *Fraxinus* (Table 2.1).

Although shade tolerance (*Acer>Fraxinus>Betula*), competition tolerance (*Betula>Fraxinus>Acer*) and cold tolerance (*Betula>Acer>Fraxinus*) were likely to have been significant determinants of seedling distribution, alternative habitat characteristics may have also contributed to patterns of seedling recruitment. *Acer*, for example, fails to regenerate on heavy, wet clay soils where *Fraxinus* regenerates

freely (Jones, 1945). *Fraxinus*, however, has less tolerance of soil acidity than *Acer* and *Betula*, failing to regenerate on soils of less than pH 4.2. Species may have also differed in susceptibility to drought stress (Peterken, 1966), soil disturbance (Evans, 1988), damping-off disease (Wardle, 1959; Tapper, 1992), inadequate soil nutrients and mycorrhizal associates (Goldberg, 1985) and the smothering and toxic action of decaying plant material overlying seedlings (Watt, 1919). A complexity of such factors most likely accounted for variation between tree species in patterns of seed germination and seedling emergence, establishment and survival.

As a result of sample size constraints, it was not possible to determine the equivalent environmental correlates of *Ilex*, *Sorbus*, *Taxus* and *Ulmus* seedling distribution. However, previous studies of regeneration in temperate deciduous woodland have identified unique regeneration characteristics for each species (Table 2.1). Seedlings of *Ilex* are highly shade tolerant (Pigott, 1983) and often widespread in the understorey (Peterken & Lloyd, 1967). In fact, seedlings are sufficiently robust to withstand the smothering and shade of *P. aquilinum*, the cover of which suppresses competitive herb growth and prevents desiccation (Peterken, 1966). Very heavy shade and litterfall beneath dense canopy cover may be sufficient to limit seedling growth, development and survival (Peterken, 1966). *Ilex* is also intolerant of drought and prolonged waterlogging (Peterken & Lloyd, 1967). Although vegetative spread may be significant for establishment in canopy gaps, it is ineffective as a mechanism of dispersal and spread (Peterken & Lloyd, 1967).

Although Evans (1988) describes *Sorbus* as a 'light demanding pioneer', seedlings of this taxon are highly shade tolerant and able to grow and survive beneath deep understorey and canopy cover (Pigott, 1983). *Taxus* is also highly tolerant of cover, although shade may limit seedling growth. Melzack & Watts (1982) found that seeds often germinated beneath the scrub cover of *Crataegus monogyna* and *Juniperus communis* when there was little sign of *Taxus* regeneration beneath canopy cover or gaps. This was consistent with the microsite-limited regeneration of *Taxus* reported by Hulme (1996a) in sites where patterns of seedling distribution were not obscured by the intensity of seed predation. *Ulmus* regenerates most profusely on moist, relatively fertile, basic soils with moderate exposures of bare soil and tree litter (Grime *et al.*, 1988). Seedlings are sensitive to drought and shade, which may limit recruitment.

It was apparent that the occurrence of early regeneration, even if profuse, was no indication of subsequent establishment. The spatial distribution of seedling recruitment was ultimately determined by mortality factors acting on seed survival and germination, and seedling emergence, growth and survival. There was strong evidence that habitat characteristics, including canopy and field layer cover, were significant determinants of seedling distribution, according to age- and species-specific tolerances. Seedlings were most likely susceptible to a greater intensity of mortality factors with decreasing age and depth of rooting (Peterken, 1966; Tapper, 1992). Supporting previous studies of natural seedling regeneration in temperate deciduous woodland, field layer cover, or a correlated factor, was the most significant habitat characteristic influencing spatial patterns of seedling recruitment. Free from the constraints of the field layer, seedlings had a much greater probability of persistence beneath the canopy (Gardner, 1977).

Variation between species in viable seed production, seed germination and seedling emergence, growth and survival reflect the diversity of established strategies and regeneration characteristics of temperate deciduous woodland trees. Differences were reflected in the dynamics of natural seedling regeneration and exemplified in the production of vast numbers of small, widely dispersed seeds and short-lived seedlings of *Betula*, relative to the production of fewer, large seeds and long-lived seedlings of *Acer* and *Fraxinus*.

CHAPTER 7

GENERAL DISCUSSION

7.1. POST-DISPERSAL SEED PREDATION AND SEEDLING HERBIVORY

Rodents were the principal agents responsible for post-dispersal seed predation, whereas background seed loss and that attributable to invertebrates and other categories of seed predator was of minor importance (Chapters 3 and 4). Seedling herbivory was attributable to a mixed suite of herbivores including invertebrates, rodents and larger mammals (Chapter 5). Mammals encountered seedlings more frequently than invertebrates, and once encountered, inflicted a greater severity of damage.

Variation in post-dispersal seed predation and seedling herbivory has been a consistent factor in all of the studies in which it has been investigated (Tables 3.1, 4.1 and 5.1). In the present study, rates of seed predation and seedling herbivory varied significantly between tree species (Chapters 3 and 5), reflecting selective, rather than random, foraging decisions. The consistency of such decisions was demonstrated in seed predation trials, when tree species were ranked in the same order in both study sites. Variation in seed predation and seedling herbivory between tree species most likely reflected individualistic, trade-off responses to the chemical (olfactory conspicuousness, nutritional value, toxicity) and physical (size, toughness, handling time) attributes of seeds and seedlings, according to dietary requirements, familiarity, tolerance of plant defence mechanisms and the availability of alternative resources. If rates of seed predation and seedling herbivory were sufficiently high to limit plant recruitment, variation between tree species may have been a significant factor regulating woodland community composition.

Seed predation and seedling herbivory also varied significantly between microhabitats (Chapters 3 and 5). Fine-scale spatial heterogeneity reflected patterns of rodent foraging in response to microhabitat characteristics, particularly the distribution of protective vegetation cover and the availability of food. Schupp (1995) considered patterns of differential patch-suitability across the landscape at seed and seedlings stages and described a continuum ranging from full concordance to full discordance. In the present study, patterns of seed and seedling survival were broadly

concordant, with rates of seed predation and seedling herbivory greater beneath protective vegetation cover than in open microhabitats. Differential foraging and offspring survival over a species' seed shadow may have a significant impact on spatial patterns of plant recruitment (Anderson, 1987; Harmon & Stamp, 1992) and may account for the spatial dissociation between natural seedling survival and field layer cover (Chapter 6).

Variation in seed predation according to seed density and distance from the parent was species-dependent (Chapter 4). Density-dependent seed survival was supported by two of five tree species, whereas distance-dependent survival was not supported by any species at a spatial scale consistent with the 'herbivore-escape hypothesis'. Overall, patterns of density- and distance-dependent seed survival were unpredictable and could not be generalised temporally or spatially for alternative plant species and predator groups. In natural populations with overlapping seed shadows, variation in seed production, seed dispersal and predator density are likely to generate a temporally dynamic association between post-dispersal seed predation and mortality-mediated tree spacing (Hubbell, 1980). In the present study, adult populations of each study species were either randomly distributed or spatially aggregated (Table 2.3), supporting the absence of predictable spacing mechanisms mediated by distance- and density-dependent predation.

7.2. RELATIVE IMPACT OF HERBIVORES ON NATURAL REGENERATION

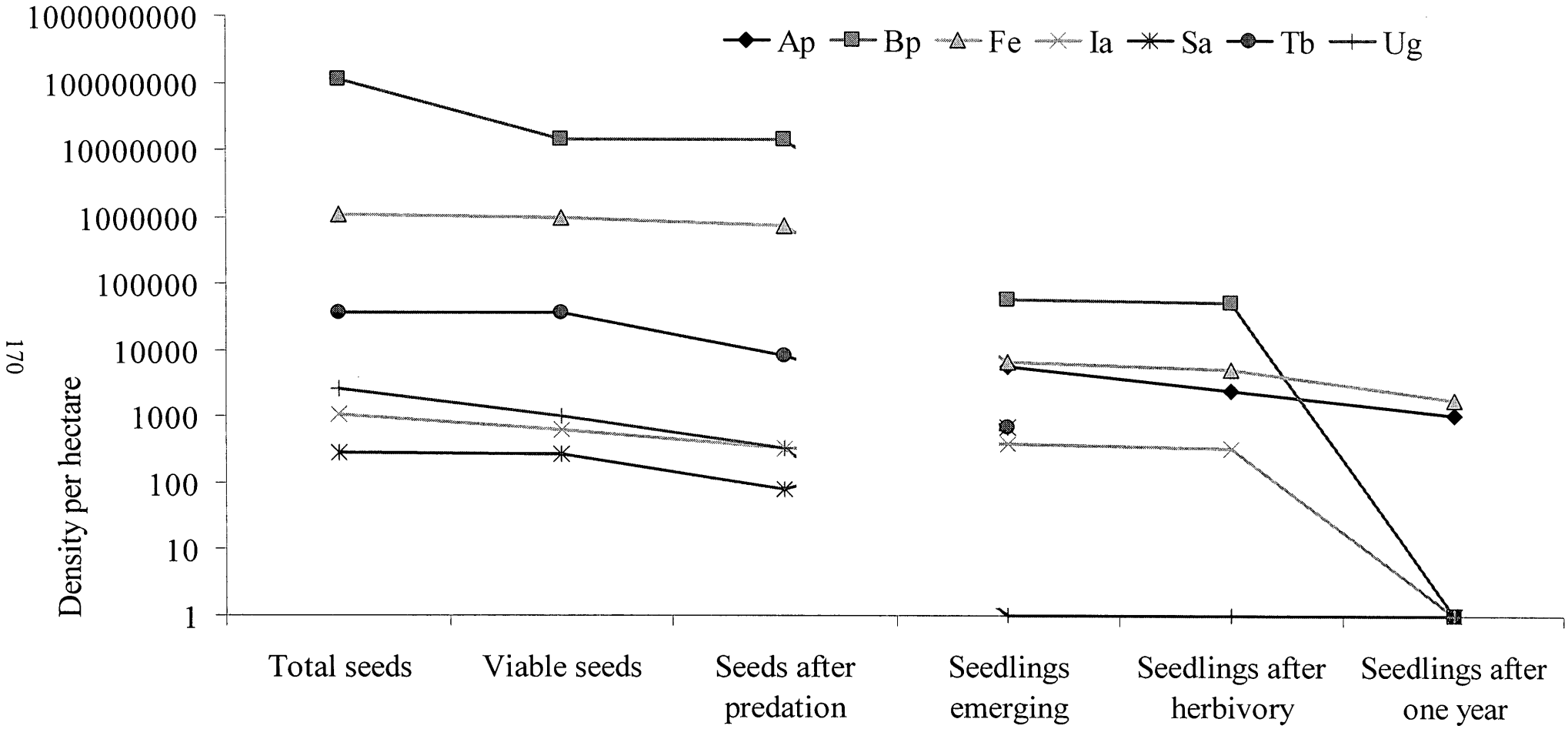
High rates of seed predation and seedling herbivory do not alone constitute evidence that herbivores influence plant regeneration dynamics. An assessment of the impact herbivores have on natural tree regeneration must consider the broader context of the regeneration sequence, including seed production, seed viability, seedling emergence and seedling survival. The natural regeneration dynamics of each study species are summarised in Table 7.1 and represented schematically in Figure 7.1, based on estimates of total seed production (1997, Chapter 6), seed viability (1997, Chapter 3), seed predation (1995-1996, Chapter 3), natural seedling emergence (1996, Chapter 6), seedling herbivory (1997, Chapter 5) and natural seedling survival (1997, Chapter 6) in Shipley Wood. Greater than ten per cent seedling damage was assumed to result in seedling mortality. Since all parameters were likely to have varied spatially and temporally and no attempt was made to assess the herbivore tolerance or

Table 7.1. Summary of parameters constituting the natural regeneration sequence of each study species in Shipley Wood (SW) and Derwent Gorge (DG). The general terms used to describe the relative magnitude of each parameter for each study species relate within columns and not between columns.

Taxon	Seed production	Seed viability	Seed encounter (Open depots)		Seed exploitation (Open depots)		'Germinant' seedling density		Seedling survival
	SW	SW	SW	DG	SW	DG	SW (1996)	SW (1997)	SW
Acer	---	---	---	---	---	---	High	Low	High
Betula	Very High	Very Low	Very Low	Low	Low	Low	Very High	Very High	Low
Fraxinus	High	Very High	Moderate	Moderate	Moderate	Low	High	Moderate	Very High
Ilex	Low	Moderate	High	High	High	High	Low	Absent	Low
Sorbus	Low	Very High	High	High	Very High	Very High	Low	Low	Low
Taxus	Low	Very High	Very High	High	Very High	Very High	Low	Absent	Low
Ulmus	Low	Low	High	High	Very High	Very High	Absent	Absent	---

Taxon	Seedling encounter (Open depots)	Seedling damage (Open depots)	'Persistent' seedling density	Sapling density		Adult density		Past regeneration	
	SW	SW	SW	SW	DG	SW	DG	SW	DG
Acer	High	Moderate	Low	High	High	High	High	Continuous	Continuous
Betula	Very Low	Moderate	Absent	Low	Low	High	Low	Limited recent	Continuous
Fraxinus	Low	Moderate	High	Very High	Moderate	High	Moderate	Continuous	Continuous
Ilex	Very Low	Low	Absent	Low	Low	Low	Low	(Limited past)	Continuous
Sorbus	---	---	Absent	Low	Absent	Low	Low	Continuous	Limited recent
Taxus	---	---	Low	Absent	Absent	Low	Low	Limited recent	Limited recent
Ulmus	High	Moderate	Absent	High	Low	Low	Low	(Limited past)	Continuous

Figure 7.1. Schematic diagram representing the natural regeneration dynamics of each study species.



recovery potential of seedlings, such data can only approximate general patterns and can by no means represent a continuous regeneration sequence. It would be particularly inappropriate to directly associate the post-dispersal survival of seeds from a known source with the natural emergence of seedlings from an unknown source to infer rates of seed germination. However, schematic representation may distinguish the general regeneration dynamics of each tree species and the relative impact of seed predation and seedling herbivory. The following discussion of natural regeneration dynamics is based on data summarised in Table 7.1 and Figure 7.1.

7.2.1. Natural regeneration dynamics of *Acer*

Although the production, viability and predation of *Acer* seeds were not quantified in the present study, Jensen (1985) recorded rates of *Acer* seed removal after three days that were more than twice as great as rates of *Betula*, *Fraxinus* and *Ulmus* seed removal. The emergence and survivorship of *Acer* seedlings was high. Moderate rates of seedling herbivory reduced seedling density by fifty-eight per cent. Alternative mortality factors accounted for the loss of a further twenty-three per cent over the following year. Although seedlings were numerous after one year and sapling density was high, the density of seedlings greater than one year old was low. Seed predation and seedling herbivory were likely to have been more limiting to the natural regeneration of *Acer* than first-year seedling mortality arising from alternative biotic and abiotic factors.

Seedlings of *Acer* are widely distributed on bare or lightly shaded, basic, low disturbance soils of adequate phosphate, moisture and depth (Evans, 1988; Grime *et al.*, 1988). Although *Acer* regenerates profusely beneath moderately deep canopy and field layer cover, in association with shade herb species, seedlings are intolerant of competition and may be readily suppressed by field layer vegetation (Jones, 1945). *Acer* seedlings typically establish beneath a thin and discontinuous layer of herbaceous species and litter (Jones, 1945), reflected in the negative association between seedling survival and field layer cover (Chapter 6). The interception of precipitation (Linhart & Whelan, 1980), removal of soil moisture and nutrients (Evans, 1988), smothering and toxic action of field layer vegetation (Watt, 1919) may have also limited recruitment. Overall, the natural regeneration of *Acer* (to first year seedlings) was more likely to have been herbivore-limited than microsite-limited in the present study, although no mortality factor was sufficient to completely restrict

recent regeneration in either study site (Figure 2.5). Herbivory may also account for the spatial dissociation between natural seedling survival and field layer cover (Chapter 6). Data were not available to assess the extent of seed-limitation.

7.2.2. Natural regeneration dynamics of *Betula*

Although total seed production by adult trees of *Betula* was very high, very low viability reduced seed density by eighty-seven per cent. Very low rates of seed predation reduced seed density by only a further half of one per cent. Although the emergence of *Betula* seedlings was very high, seedling survivorship was low. Very low rates of seedling herbivory reduced seedling density by thirteen per cent. Alternative mortality factors accounted for the loss of the remaining eighty-seven per cent of seedlings over the following year. No seedlings greater than one year old and few saplings of *Betula* were recorded. Seed production, seed predation and seedling herbivory were likely to have been less limiting to the natural regeneration of *Betula* than seed viability and first-year seedling mortality arising from alternative biotic and abiotic factors.

Betula regenerates most profusely on open mineral soil of moderate phosphate status (Evans, 1988), often with continuous moss cover or a thin layer of tree litter (Grime *et al.*, 1988). Seedlings of *Betula* are cold resistant and have some degree of competition tolerance, although are intolerant of shade and drought (Table 2.1). Light-demanding seedlings of *Betula* typically establish beneath openings in both main and understorey canopies (Morgan, 1991), showing a marked dissociation from ungrazed field layers and heavily shaded sites (Chapter 6). The interception of precipitation (Linhart & Whelan, 1980), removal of soil moisture and nutrients (Evans, 1988), smothering and toxic action of field layer vegetation (Watt, 1919) may have also limited recruitment. Overall, the natural regeneration of *Betula* (to first year seedlings) was more likely to have been microsite-limited than seed- or herbivore-limited in the present study. Absence of suitable regeneration microsites may account for limited recent regeneration in Shipley Wood (Figure 2.6).

7.2.3. Natural regeneration dynamics of *Fraxinus*

The total production of *Fraxinus* seeds was high and very high seed viability reduced seed density by only eleven per cent. Low rates of seed predation reduced seed density by a further twenty-two per cent. The emergence of *Fraxinus* seedlings

was high and seedling survivorship was very high. Low rates of seedling herbivory reduced seedling density by twenty-two per cent. Alternative mortality factors accounted for the loss of a further fifty-two per cent of seedlings over the following year. Seedlings were numerous after one year, as were seedlings greater than one year old and saplings. Seed production, seed viability, seed predation and seedling herbivory were likely to have been less limiting to the natural regeneration of *Fraxinus* than first-year seedling mortality arising from alternative biotic and abiotic factors.

Fraxinus regenerates most profusely on relatively open, moist, well drained, base-rich sites with thin litter layers (Grime *et al.*, 1988; Peltier *et al.*, 1997). Seedlings of *Fraxinus* are sensitive to drought, competition and late frost (Table 2.1) and intolerant of dense shade (Wardle, 1961), reflected in the negative association between seedling survival and field layer cover (Chapter 6). The interception of precipitation (Linhart & Whelan, 1980), removal of soil moisture and nutrients (Evans, 1988), smothering and toxic action of field layer vegetation (Watt, 1919) may have also limited recruitment. Overall, the natural regeneration of *Fraxinus* (to first year seedlings) was more likely to have been microsite-limited than seed- or herbivore limited in the present study, although no mortality factor was sufficient to completely restrict recent regeneration in either study site (Figure 2.7).

7.2.4. Natural regeneration dynamics of *Ilex*

The total production of *Ilex* seeds was low and moderate seed viability reduced seed density by forty-two per cent. Moderate rates of seed predation reduced seed density by a further twenty-seven per cent. The few seedlings of *Ilex* that did emerge had low rates of survivorship and no seedlings survived after one year. Very low rates of seedling herbivory reduced seedling density by fifteen per cent. Alternative mortality factors accounted for the loss of the remaining eighty-five per cent of seedlings over the following year. No seedlings greater than one year old and few saplings of *Ilex* were recorded. Seed predation and seedling herbivory were likely to have been less limiting to the natural regeneration of *Ilex* than seed production, seed viability and first-year seedling mortality arising from alternative biotic and abiotic factors.

Seedlings of *Ilex* are sensitive to late frost and intolerant of drought and prolonged waterlogging (Peterken & Lloyd, 1967; Table 2.1). Although *Ilex* seedlings

are highly shade tolerant (Pigott, 1983) and often widespread in the understorey (Peterken & Lloyd, 1967), very heavy shade and litterfall beneath dense canopy cover may be sufficient to limit seedling growth, development and survival (Peterken, 1966). Overall, the natural regeneration of *Ilex* (to first year seedlings) was more likely to have been microsite-and seed-limited than herbivore-limited in the present study, although no mortality factor was sufficient to completely restrict recent regeneration in either study site (Figure 2.8).

7.2.5. Natural regeneration dynamics of *Sorbus*

Although the total production of *Sorbus* seeds was low, seed viability was very high, reducing seed density by only six per cent. However, subsequent seed predation was high, reducing seed density by a further sixty-five per cent. The few seedlings of *Sorbus* that did emerge had low rates of survivorship and no seedlings survived after one year. Although the herbivory of *Sorbus* seedlings was not quantified in the present study, Sviridenko (1940, cited in Golley *et al.*, 1975) recorded rates of *Sorbus* seedling herbivory that were similar to rates of *Fraxinus* seedling herbivory and significantly lower than rates of *Acer* and *Ulmus* seedling herbivory. No seedlings greater than one year old and few saplings of *Sorbus* were recorded. Seed production, seed predation and first-year seedling mortality arising from alternative biotic and abiotic factors were likely to have been more limiting to the natural regeneration of *Sorbus* than seed viability and seedling herbivory.

Although Evans (1988) describes *Sorbus* as a 'light demanding pioneer', *Sorbus* seedlings are highly shade tolerant and able to grow and survive beneath deep understorey and canopy cover (Pigott, 1983; Table 2.1). Overall, the natural regeneration of *Sorbus* (to first year seedlings) was likely to have been seed-, herbivore- and microsite-limited in the present study, which may account for limited recent regeneration in Derwent Gorge (Figure 2.9).

7.2.6. Natural regeneration dynamics of *Taxus*

Although the viability of *Taxus* seeds was very high, total seed production was low. High rates of seed predation reduced seed density by a further seventy-seven per cent. The few seedlings of *Taxus* that did emerge had low rates of survivorship and no seedlings survived after one year. Seedlings greater than one year old were rare and no saplings of *Taxus* were recorded. Although seedling herbivory could not be

distinguished from first-year seedling mortality arising from alternative biotic and abiotic factors, seed production and seed predation were likely to have been more limiting to the natural regeneration of *Taxus* than seed viability.

Seedlings of *Taxus* are highly shade tolerant, although sensitive to cold stress (Table 2.1). Overall, the natural regeneration of *Taxus* (to first year seedlings) was more likely to have been seed- and herbivore-limited than microsite-limited in the present study. Herbivory and low viable seed production may account for limited recent regeneration in Shipley Wood and Derwent Gorge (Figure 2.10). Recruitment may be associated with scrub cover (microsite-limited) when patterns of seedling distribution are not obscured by the intensity of herbivory (Melzack & Watts, 1982; Hulme, 1996a).

7.2.7. Natural regeneration dynamics of *Ulmus*

The total production of *Ulmus* seeds was low and low seed viability reduced seed density by sixty-two per cent. High rates of seed predation reduced seed density by a further twenty-six per cent. Although naturally emerged seedlings of *Ulmus* were not recorded, rates of herbivory of artificially supplied seedlings were moderate. Seedlings greater than one year old were also absent, whereas the density of *Ulmus* saplings was high. Although seedling herbivory could not be distinguished from first-year seedling mortality arising from alternative biotic and abiotic factors, seed production and seed viability were likely to have been more limiting to the natural regeneration of *Ulmus* than seed predation.

Ulmus regenerates most profusely on moist, relatively fertile, basic soils with moderate exposures of bare soil and tree litter (Grime *et al.*, 1988). Seedlings of *Ulmus* are sensitive to shade and intolerant of drought (Table 2.1). Overall, the natural regeneration of *Ulmus* (to first year seedlings) was more likely to have been seed- and microsite-limited than herbivore-limited in the present study, although no mortality factor was sufficient to completely restrict recent regeneration in either study site (Figure 2.11).

7.3. ACTUAL IMPACT OF HERBIVORES ON NATURAL REGENERATION

Although seed predation and seedling herbivory may be relatively important to the natural regeneration of certain tree taxa, particularly *Acer*, *Sorbus* and *Taxus*, the actual impact of herbivores may be less significant. Herbivore-mediated plant

mortality may have only replaced mortality that would have otherwise occurred during natural self-thinning, having little overall effect on plant regeneration dynamics. Alternatively, herbivore-mediated mortality may have ameliorated intraspecific competition between plants by reducing density and increasing overall rates of survival.

In addition to when plant recruitment is microsite-limited rather than seed- or herbivore-limited (Hulme, 1996a), herbivores are unlikely to influence natural regeneration dynamics when plants regenerate by vegetative expansion or satiate seed predators with mast seed crops (Jensen, 1982) or when banks of dormant seeds or the repeated, prolonged reproduction of long-lived iteroparous species compensate for seed and seedling loss to herbivores (Crawley, 1983).

The natural regeneration of *Acer* (to first year seedlings) was more likely to have been herbivore-limited than microsite-limited. Although *Acer* does not achieve vegetative expansion or regenerate from a persistent seed bank, adults do produce vast numbers of seeds in mast years, typically every one to three years (Evans, 1988). With repeated, prolonged reproduction over a life span of 400-600 years, *Acer* is unlikely to be critically dependent on current regeneration.

The natural regeneration of *Betula* (to first year seedlings) was more likely to have been microsite-and seed-limited than herbivore-limited. Although *Betula* does not achieve vegetative expansion, adults do produce vast numbers of small seeds in mast years, typically every one to three years (Evans, 1988), which may have limited persistence on or near the soil surface. *Betula* depends on opportunistic, gap-phase regeneration, supported by repeated, prolonged reproduction and consistent with microsite-limited recruitment. Adults of *Betula* are relatively short-lived (c.60-70 years) and are soon out-competed by successional taxa.

The natural regeneration of *Fraxinus* (to first year seedlings) was more likely to have been microsite-limited than seed- or herbivore limited. Although *Fraxinus* does not achieve vegetative expansion, adults do produce vast numbers of seeds in mast years, typically every two to five years (Wardle, 1961; Evans, 1988), which has the effect of satiating rodent seed predators (Chapter 4). The persistence of viable seeds on the soil surface for up to six years may also facilitate gap-phase regeneration. With repeated, prolonged reproduction over a life span of approximately 180 years

(>300 years if coppiced), *Fraxinus* is unlikely to be critically dependent on current regeneration.

The natural regeneration of *Ilex* (to first year seedlings) was more likely to have been microsite-and seed-limited than herbivore-limited. There is also some evidence that *Ilex* achieves vegetative expansion when leafy stems detached by herbivores root when covered by moist litter (Peterken & Lloyd, 1967). Although vegetative spread may be locally important in colonising canopy gaps, along with regeneration involving a bank of persistent seedlings, it is ineffective as a mechanism of dispersal. With repeated, prolonged reproduction over a life span of 250-300 years, *Ilex* is unlikely to be critically dependent on current regeneration. Good fruit years correlate with July radiance and air temperature of the previous year and the absence of severe late spring frost (Peterken & Lloyd, 1967).

The natural regeneration of *Sorbus* (to first year seedlings) was likely to have been seed-, herbivore- and microsite-limited. Although *Sorbus* does not achieve vegetative expansion, seeds may have considerable longevity in the soil (Hill, 1979). With repeated, prolonged reproduction over a life span of up to 150 years, *Sorbus* is unlikely to be critically dependent on current regeneration.

The natural regeneration of *Taxus* (to first year seedlings) was more likely to have been seed- and herbivore-limited than microsite-limited. *Taxus* does not achieve vegetative expansion or regenerate from a persistent seed bank. However, with repeated, prolonged reproduction over a life span that may exceed 1000 years, *Taxus* is unlikely to be critically dependent on current regeneration.

The natural regeneration of *Ulmus* (to first year seedlings) was more likely to have been seed- and microsite-limited than herbivore-limited. *U. glabra* does not achieve vegetative expansion or regenerate from a persistent seed bank. However, with repeated, prolonged reproduction over a life span of more than 200 years, *Ulmus* is unlikely to be critically dependent on current regeneration.

Even very low rates of regeneration occurring intermittently over the long life span of tree species may be sufficient to maintain mixed-age populations. Rates of seed predation and seedling herbivory would have to be at a sufficiently high intensity over a sufficiently long period, relative to the life span of the species, for herbivores to have a real impact on natural regeneration, plant distribution and community composition in temperate deciduous woodland. Even when overall rates of seed

predation and seedling herbivory are intense, differential foraging and offspring survival over a species' seed shadow may be sufficient to maintain plant recruitment and population density. Recruitment may be restricted to open microhabitats, for example, where rates of seed and seedling survival are proportionally higher than alternative microhabitats (Chapters 3, 5 and 6). The burial of seeds beneath litter or soil may also be an effective means of escaping seed detection and predation (Hulme, 1993), as well as reducing desiccation (Watt, 1919) and increasing seedling yields (Shaw, 1968b). Foraging mammals may have an important role in burrowing and trampling seeds in to the soil (Shaw, 1968b; Evans, 1988). The ability of plants to compensate for losses or invest in anti-predator defence is an important factor influencing the impact of herbivores on plant regeneration and evolution.

Limited current regeneration was most pronounced for *Taxus*, which was also the most likely of the study taxa to be herbivore-limited. Hulme (1996a) recorded similar unimodal age-distribution patterns and high rates of seed predation within *Fraxinus-Acer* woodlands in County Durham, with peak regeneration occurring between 150 and 200 years ago. While it is possible to quantify herbivory and identify patterns of variation from short-term studies, problems arise when results are extrapolated to make generalisations regarding the impact of herbivores on the natural regeneration dynamics of long-lived tree species. Although it may be difficult to identify herbivory as the principal factor regulating natural regeneration dynamics in temperate deciduous woodland, it was apparent that for a number of tree species, herbivores accounted for a significant proportion of plant mortality. The coaction of herbivory and alternative biotic and abiotic mortality factors is more likely to determine patterns of natural regeneration. The relative impact of each factor can only be distinguished by integrating historical patterns of regeneration with long-term field investigations conducted at a temporal scale more appropriate to life span of the species under investigation.

7.4. FURTHER CONSIDERATIONS

Short-term trials investigating the predation of experimentally supplied seeds and seedlings were likely to have over- or under-estimated natural rates of predation, making general conclusions regarding the actual impact of herbivores on natural regeneration more difficult. Alternative studies have followed the long-term survival

of naturally dispersed seeds and seedlings as an effective means of quantifying herbivore-mediated plant mortality (Table 3.1). However, predation trials allowed the experimental manipulation necessary to investigate relative variation in seed predation and seedling herbivory according to tree species, predator group, site, microhabitat, seed density and distance from the parent.

The elimination of herbivory using large, selective exclosure treatments may have been a more effective means of demonstrating the long-term effects of herbivores on natural regeneration, community composition and plant distribution. However, subsequent changes in recruitment dynamics would not have elucidated the relative impact of herbivores at each stage of the regeneration sequence, as was the aim of detailed field-based investigations comprising the present study. In addition, herbivore exclusion would not distinguish the indirect effect of herbivores on field layer vegetation from the direct effect of herbivores on seed and seedling survival. However, indirect effects are an important aspect of regeneration dynamics, and a long-term exclosure-based investigation would undoubtedly provide important information regarding the overall impact of herbivores on natural regeneration.

7.5. WOODLAND MANAGEMENT

Although it was difficult to make generalisations regarding the impact of herbivores on natural regeneration dynamics, relative to seed- and microsite-limitations, it was recognised that the current regeneration of a number of tree species was limited. With populations declining throughout most of its European range, the restricted current regeneration of *Taxus* in Shipley Wood, Derwent Gorge and elsewhere in County Durham (Hulme, 1996a) was of particular concern.

Shaw (1968b) proposed that high rates of herbivore-mediated plant mortality may be alleviated by; 1) a reduction in the population of seed and seedling predators, particularly small mammals, 2) the exclusion of domestic grazing animals and 3) the disturbance of surface layers of the soil and an increase in the retention and even distribution of tree litter to enhance seed burial, seed survival and seed germination. Although fencing may afford protection from large mammals, tree shelters have become the most effective means of protecting young regeneration from small and large mammals (Evans, 1988).

Further preparatory measures that improve the success of natural regeneration include the provision of a plentiful seed supply and ground conditions that favour

seed germination and seedling survival (Evans, 1988). Bare, moist soils that are not eroding or compacted are favoured. Although light, discontinuous field layer vegetation improves litter retention and soil activity, dense cover may limit recruitment by the interception of light and precipitation, the removal of moisture and nutrients from the soil and the smothering and toxic action of decaying plant material overlying seedlings (Watt, 1919). Field layer vegetation may also harbour rodent seed and seedling predators (Chapters 3 & 5), whereas scrub understorey may protect seedlings from larger herbivores (Morgan, 1991). The availability of scrub cover, including *Crataegus monogyna* and *Juniperus communis*, may be particularly important to the natural regeneration of *Taxus baccata* (Melzack & Watts, 1982; Hulme, 1996a).

Successful regeneration management would require partial or full removal of the field layer (Goldberg, 1985; Tapper, 1992). Light grazing and the manipulation of shade cast by the overstorey canopy are both effective means of controlling field layer vegetation, and grazing animals may also turn over the soil and tread in seeds as a further aid to natural regeneration (Shaw, 1968b; Evans, 1988). Although grazing, browsing and trampling by large animals reduce seedling establishment and sapling survival, such activities may be necessary to suppress the dominance of *Rubus fruticosus* (bramble) that would otherwise shade the soil almost entirely and limit the establishment of woody and herbaceous species (Linhart & Whelan, 1980). The historical practice of pannage, where pigs rooting for fungi and mast turn over the soil, tread in seeds and expose the seed bank, may also have a significant role in natural regeneration management. The disturbance of vegetation and top soil by *Sus scrofa* (wild boar) may also increase local plant species richness (Milton *et al.*, 1997), although Bruinderink & Hazebroek (1996) found no effect of rooting on the regeneration of coniferous and deciduous tree species, including *Betula pendula*, *Sorbus aucuparia* and *Ilex aquifolium*.

The control of field layer vegetation and the exposure of loosened, mulched, mineral seedbeds should be achieved in the autumn of a good seed year to maximise regenerative success. Subsequent management may include the removal of unwanted woody growth that may threaten regeneration, combined with respacing of young trees where dense regeneration becomes self-limiting (Evans, 1988).

The present study supports the principles that woodland conservation and management is critically dependent on an understanding of tree population dynamics (Peterken, 1993), that natural regeneration has a central role in plant demography (Watt, 1919, 1923; Peterken & Tubbs, 1965; Grubb, 1977) and that the reasons for inadequate regeneration are many and complex. Investigating the magnitude and variability of seed production, seed survival and seedling survival has further elucidated the impact of seed-, microsite- and herbivore-limitations on the natural regeneration of tree species that form the framework of these communities (Hulme, 1996a). Since natural regeneration is known to be severely deficient or absent in many temperate deciduous woodlands (Watt, 1919, 1923; Peterken & Tubbs, 1965; Shaw, 1968a,b; Linhart & Whelan, 1980; Evans, 1988; Hulme, 1996a), factors contributing to plant mortality at seed and seedling stages should be carefully considered in woodland management plans aiming to conserve native woodlands and the remainder of a diverse flora and fauna once typical of much of the country (Linhart & Whelan, 1980).

The Bialowieza Forest, Poland, contains the most extensive stands of primeval temperate woodland in Europe (Mitchell & Cole, 1998). Surviving fragments of old-growth forest may provide an important model for understanding the dynamics of forest communities and ecosystems. In Bialowieza, large herbivores, including *Bison bonasus* (European bison), *Alces alces* (moose), *Cervus elaphus* (red deer), *Capreolus capreolus* (roe deer) and *Sus scrofa* (wild boar), and their natural predators, including *Canis lupus* (wolf) and *Lynx lynx* (lynx), are recognised as having a central role in temperate forest dynamics (Falinski, 1988; Okarma *et al.*, 1995). The extinction of herbivore species and the current imbalance between herbivore populations and their natural enemies may significantly contribute to the recent deficiency of natural regeneration in many semi-natural temperate deciduous woodlands. Since natural regeneration is at least partially regulated by plant-herbivore interactions, the potential benefit of reintroducing extinct herbivore species that provide the ground conditions necessary for regeneration and reinstating the natural regulation of herbivore populations, should be carefully considered. A long-term, mixed management strategy that recognises the beneficial and detrimental impacts of herbivores on natural regeneration dynamics is likely to be the most effective means of supporting the conservation of seed-, microsite- and herbivore-limited tree species in temperate deciduous woodland.

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